Pr 260 C1

Acta Myriapodologica

Edited by
Jean-Jacques GEOFFROY
Jean-Paul MAURIÈS
Monique NGUYEN DUY-JACQUEMIN

COM

MÉMOIRES DU MUSÉUM NATIONAL D'HISTOIRE NATURELLE
TOME 169
1996

MÉMOIRES DU MUSÉUM NATIONAL D'HISTOIRE NATURELLE

Rédacteur en chef (*Editor-in-Chief*) : Jean-Lou JUSTINE

Rédacteurs (*Editors*) : Jean-Marie BETSCH, Philippe BOUCHET, Christian ÉRARD & Jean-Lou JUSTINE

Assistante de rédaction (*Copy editor*) : Bernadette CHARLES

Adresse (*Address*)

Mémoires du Muséum national d'Histoire naturelle

57, rue Cuvier

F-75005 Paris

Tél. : [33] (1) 40 79 34 37

Fax. : [33] (1) 40 79 38 08

e-mail : memoires@mnhn.fr

Les *Mémoires du Muséum national d'Histoire naturelle* publient des travaux originaux majeurs, tels que des monographies ou des volumes à auteurs multiples. Les auteurs sont invités, pour toutes les questions éditoriales, à prendre contact avec le directeur de la publication. Les manuscrits peuvent être en français ou en anglais.

The Mémoires du Muséum national d'Histoire naturelle *publishes major original contributions, such as monographs or multi-authored volumes. Prospective authors should contact the Editor-in-Chief. Manuscripts in French or English will be considered.*

Vente en France :

MUSÉUM NATIONAL D'HISTOIRE NATURELLE
SERVICE DES PUBLICATIONS SCIENTIFIQUES
Diffusion : Delphine HENRY
57, rue Cuvier
F-75005 Paris
Tél. : [33] (1) 40 79 37 00
Fax : [33] (1) 40 79 38 40

Sales Office:

UNIVERSAL BOOK SERVICES

Dr W. BACKHUYS
P.O. Box 321
NL-2300 AH Leiden
The Netherlands
Tel. : [31] (71) 517 02 08
Fax : [31] (71) 517 18 56

Parution et prix irréguliers. Les ordres permanents d'achat et les commandes de volumes séparés sont reçus par le **Service des Publications Scientifiques, Diffusion** (pour la France et les DOM-TOM uniquement), ou par **Universal Book Services**. Catalogue sur demande. Une liste des derniers titres parus figure en page 3 de couverture.

Volumes are published at irregular intervals, and at irregular prices. Standing orders and orders for single volumes should be directed to the ***Service des Publications Scientifiques du Muséum****, (France and DOM-TOM only) or* ***Universal Book Services****. Price list and catalogues are available on request. Recently published memoirs are listed on page 3 of the cover.*

Printed on acid-free paper
Imprimé sur papier non acide

Source : MNHN, Paris

Bibliothèque Centrale Muséum
3 3001 00125732 7
Source : MNHN, Paris

Source : MNHN, Paris

P. 280 c 1

Source : MNHN, Paris

Cover illustration:

Orthomorpha coarctata Saussure, 1860, a widespread polydesmid millipede in the field, French Guiana: Diplopoda, Polydesmida, Paradoxosomatidea (photograph by Michel BOULARD).

Illustration de couverture :

Orthomorpha coarctata *Saussure, 1860, diplopode polydesmide ubiquiste photographié sur le vif en Guyane Française : Diplopoda, Polydesmida, Paradoxosomatidea (photographie de Michel BOULARD).*

Source : MNHN, Paris

Acta Myriapodologica

Source : MNHN, Paris

ISBN : 2-85653-502-X
ISSN : 1243-4442
© Éditions du Muséum national d'Histoire naturelle, Paris, 1996

PHOTOCOPIES :

Les *Mémoires du Muséum* adhèrent au Centre Français d'Exploitation du Droit de Copie (CFC), 3, rue Hautefeuille, 75006 Paris. Le CFC est membre de l'International Federation of Reproduction Rights Organisations (IFRRO). Aux États-Unis d'Amérique, contacter le Copyright Clearance Center, 27, Congress Street, Salem, Massachusetts 01970.

PHOTOCOPIES:

The Mémoires du Muséum *adhere to the Centre Français d'Exploitation du Droit de Copie (CFC), 3, rue Hautefeuille, 75006 Paris. The CFC is a member of International Federation of Reproduction Rights Organisations (IFRRO). In USA, contact the Copyright Clearance Center, 27, Congress Street, Salem, Massachusetts 01970.*

Source : MNHN, Paris

MÉMOIRES DU MUSÉUM NATIONAL D'HISTOIRE NATURELLE

TOME 169
ZOOLOGIE

Acta Myriapodologica

edited by

Jean-Jacques GEOFFROY*, Jean-Paul MAURIÈS**
& Monique NGUYEN DUY- JACQUEMIN***

* Muséum national d'Histoire naturelle
Laboratoire d'Écologie générale
4, avenue du Petit Château
F-91800 Brunoy

** Muséum national d'Histoire naturelle
Laboratoire de Zoologie, Arthropodes
61, rue Buffon
F-75231 Paris Cedex 05

*** Muséum national d'Histoire naturelle
Laboratoire de Zoologie, Arthropodes
61, rue Buffon
F-75231 Paris Cedex 05

ÉDITIONS
DU MUSÉUM
PARIS

1996

Source : MNHN, Paris

Source : MNHN, Paris

CONTENTS/SOMMAIRE

Pages

Introduction 13
Jean-Jacques GEOFFROY

List of participants and contributors 19

Allocution d'ouverture 21
Jean-Marie DEMANGE

HISTORICAL MYRIAPODOLOGY

Myriapodology before and after Martin Lister's «Journey to Paris in the Year 1698» 25
Stephen P. HOPKIN

ADVANCES IN SYSTEMATICS AND BIODIVERSITY

An approach to the revision of the East Asian millipede genus *Anaulaciulus* 35
Zoltàn KORSOS

The taxa of *Rhymogona* (Diplopoda: Craspedosomatidae): a ring species. Part one: genetic analysis of the population structure 45
Adolf SCHOLL & Ariane PEDROLI-CHRISTEN

***Rhymogona* (Diplopoda, Craspedosomatidae), un genre monospécifique. Deuxième partie : révision basée sur les résultats morphologiques, génétiques et faunistiques** 53
Ariane PEDROLI-CHRISTEN & Adolf SCHOLL

***Mastigophorophyllon* (Verhoeff,1897) et *Karpatophyllon* Jawlowsky, 1928, genres des Carpates (Chordeumatida, Diplopoda)** 61
Traian CEUCA

Sur la remarquable conformation des apophyses génitales mâles chez un polydesmide néotropical 67
Ionel TABACARU

Records of paradoxosomatid millipedes of India 73
Kubra BANO

Systematics and biogeography of *Ctenophilus* Cook, 1898. A genus of centipedes with disjunct distribution (Geophilomorpha, Schendylidae) 79
Luis A. PEREIRA

Review and perspective of study on myriapodology of China 81
Daqing WANG & Jean-Paul MAURIÈS

A taxonomic study of polydesmoid millipedes (Diplopoda) based on their mandibular structures 101
Kiyoshi ISHII & Hiroshi TAMURA

Source : MNHN, Paris

Systématique et biogéographie des diplopodes pénicillates des îles Canaries et du Cap Vert 113
Monique NGUYEN DUY - JACQUEMIN

Une approche des Diplopoda Penicillata de l'Amérique du Nord 127
Bruno CONDÉ

About the taxomomy of Spanish Scolopendrellidae 137
Maria Teresa DOMINGUEZ RODRIGUEZ

Some observations on the onychophoran fauna of Tasmania 139
Hilke RUHBERG & Robert MESIBOV

COMMUNITY STUDIES AND BIOGEOGRAPHY

Millipedes as aids for the reconstruction of glacial refugia (Myriapoda: Diplopoda) 151
Jörg SPELDA

On the distribution and faunogenesis of Himalayan millipedes (Diplopoda): Preliminary results 163
Sergei I. GOLOVATCH & Jochen MARTENS

Étude systématique et écologique des myriapodes dans le Parc National de Chréa (Atlas blidéen), Algérie 175
Ourida ABROUS-KHERBOUCHE

Étude des communautés de myriapodes (Chilopoda et Diplopoda) des forêts prépyrénéennes (Huesca, Espagne) 187
Antoni SERRA, Maria Cristina VICENTE & Eduardo MATEOS

Study of centipedes communities of three habitats in the Province of Ciudad Real .. 205
Andrès GARCIA RUIZ & Francisco J. SANTIBAÑEZ

Synanthropisation of the Diplopoda fauna of Poland 209
Wojcieh B. JEDRYCZKOWSKI

Chilopoda of urban greens in Warsaw 213
Jolanta WYTWER

Centipedes of Poznan town (Poland) 221
Malgorzata LESNIEWSKA

Contribution à la connaissance des lithobiomorphes (Chilopoda) de la région palestinienne 225
Stefan NEGREA & Zachiu MATIC (†)

Check-list, distribution and habitat in Bulgarian centipedes 235
Georgi RIBAROV

Geographical distribution of diplopods in Great Britain and Ireland; possible causal factors 243
Anthony D. BARBER & Richard E. JONES

Millipedes recorded in the Grand Duchy of Luxembourg 257
Richard Desmond KIME

Source : MNHN, Paris

Some patterns in the distribution and origin of the lithobiomorph centipede fauna of the Russian Plain (Chilopoda: Lithobiomorpha) 265
Nadezhda T. ZALESSKAJA & Sergei I. GOLOVATCH

The French Millipede Survey: towards a comprehensive inventory and cartography of the Diplopoda in France 269
Jean-Jacques GEOFFROY

Faunistique des mille-pattes de Suisse (Diplopoda) 281
Ariane PEDROLI-CHRISTEN

SYSTEMATICS AND EVOLUTION: PHYLOGENETIC RELATIONSHIPS

On myriapod / insect interrelationships 283
Otto KRAUS & Margarete KRAUS

Morphology and evolution of circulatory organs in the Tracheata 291
Günther PASS

Some problems in the systematics of the order Scolopendromorpha (Chilopoda) 293
Arkady A. SCHILEYKO

Plesiomorphic and apomorphic characters states in the class Chilopoda 299
Carol C. PRUNESCU

A preliminary study on phylogeny and biogeography of the family Paracortinidae (Myriapoda: Callipodida): a cladistic analysis 307
Daqing WANG

The penis as a phylogenetic character in the millipede family Julidae 313
Henrik ENGHOFF

REPRODUCTIVE AND DEVELOPMENTAL TRENDS IN DIPLOPODA AND CHILOPODA

Functional morphology and evolution in genitalia of Diplopoda - Helminthomorpha 327
Andreas TADLER

Sperm competition and the evolution of millipede genitalia 331
Mandy BARNETT & Steven R. TELFORD

Preliminary data on the anatomy of the genital systems in *Craterostigmus tasmanianus* (Craterostigmomorpha) and *Esastigmatobius longitarsis* (Henicopidae, Lithobiomorpha) (Chilopoda) 341
Carol C. PRUNESCU, Robert MESIBOV & Keizaburo SHINOHARA

On some structural abnormalities in *Dignathodon microcephalum* (Lucas, 1846) and their possible significance 347
Francisco J. SANTIBAÑEZ & Andrès GARCIA RUIZ

Developmental trends in the post-embryonic development of lithobiomorph centipedes 351
Alessandro MINELLI, Enrico NEGRISOLO & Giuseppe FUSCO

Source : MNHN, Paris

Étude de la reproduction et du développement post-embryonnaire de *Lithobius pilicornis* Newport, 1844 (Chilopoda, Lithobiomorpha) 359
Antoni SERRA & Maria Carme MIQUEL

Développement post-embryonnaire et cycle biologique de *Bothropolys elongatus* Newport dans l'Est Algérien 365
Tarek DAAS, Noureddine BOUZERNA & Michel DESCAMPS

The segmentation of the head and anterior trunk of millipedes (Diplopoda) - A reassessment 371
Wolfgang DOHLE

On periodomorphosis, iteroparity and life-cycles in males and females of *Tachypodoiulus niger* (Leach) (Myriapoda, Diplopoda, Julidae) in France, Germany and Great-Britain 373
François SAHLI

PHYSIOLOGY, ECOPHYSIOLOGY, CELL BIOLOGY

cAMP influence on brain and germinal cells RNA syntheses in *Lithobius forficatus* (L.) an autoradiographic study 385
Michel DESCAMPS, Catherine JAMAULT-NAVARRO & Marie-Chantal FABRE

Cadmium kinetics in *Lithobius forficatus* (L). during experimental contamination and decontamination 391
Sylvie GÉRARD, Marie-Chantal FABRE & Michel DESCAMPS

Cytochemistry of the tergite epicuticle of *Glomeris marginata* (Villers) (Myriapoda, Diplopoda): Preliminary experimental results 395
Philippe COMPÈRE, Stéphane DEFISE & Gerhard GOFFINET

Coxal organs of chilopoda: the exocrine glands in *Lithobius forficatus* 403
Jörg ROSENBERG & Hartmut GREVEN

The phenoloxidase from the hemolymph of Diplopoda 411
Willi E. R. XYLANDER

In vitro cellular immune reactions of hemocytes against bacteria and their differential degradation in myriapods 421
Lutz NEVERMANN & Willi E. R. XYLANDER

Evidence for antibacterial activity in haemolymph of Diplopoda: preliminary results 431
Grzegorz KANIA, Jan JAROSZ, Mariola ANDREJKO & Malgorzata STEFANIAK

Supernumerary malpighian tubules in chilopods 437
Carol C. PRUNESCU & Paula PRUNESCU

The structure and possible function of the spiracles of some Scolopendridae (Chilopoda, Scolopendromorpha) 441
John G. E. LEWIS, Trevor J. HILL & Gavin E. WAKLEY

Source : MNHN, Paris

Population metabolism of millipedes at two altitudinal zones in the Central Alps (Tirol, Austria) 451
Erwin MEYER, Peter MARSONER & Elisabeth FISCHER

Variation de la teneur en eau en fonction de la taille corporelle dans une population du diplopode *Polyzonium germanicum* 461
Guy VANNIER & Jean-François DAVID

The respiratory response to changing temperature in millipedes belonging to the genus *Glomeris* Latreille, 1802 473
Vladimir SUSTR

Submersion tolerance of some diplopod species 477
Klaus Peter ZULKA

Eversible vesicles in Myriapoda 483
Frantisek WEYDA

POPULATION BIOLOGY, SOIL ECOLOGY AND BEHAVIOUR

Étude comparative des techniques d'échantillonnage des macroarthropodes saprophages (Isopoda and Diplopoda) 485
Etienne BRANQUART & Charles GASPAR

Experimental behaviour of a tropical invertebrate: *Epiperipatus biolleyi* (Onychophora: Peripatidae) 493
Juliàn MONGE-NAJERA, Zaidett BARRIENTOS & Franklin AGUILAR

***Scolopendra morsitans* Linnaeus, 1758: a characteristic prey of the African carpet viper *Echis ocellatus* Stemmler, 1970** 495
Pascal REVAULT

The life cycle of *Cylindroiulus latestriatus* (Curtis, 1845) 501
Karin VOIGTLÄNDER

Life-cycle of the millipede *Melogona voigti* (Verhoeff, 1899) from a suburban forest in South Bohemia 509
Karel TAJOVSKY

Compared life-cycles and reproductive strategies in local populations of *Rossiulus kessleri* (Lohmander) (Julidae, Diplopoda) from isolated habitats 515
Bella R. STRIGANOVA

Survival strategy of the terricolous millipede *Cutervodesmus adisi* Golovatch (Fuhrmannodesmidae, Polydesmida) in a blackwater inundation forest of Central Amazonia (Brazil) in response to the flood pulse 523
Joachim ADIS, Sergei I. GOLOVATCH & Susanne HAMANN

Cycles d'activité comparés de populations de diplopodes édaphiques dans un écosystème forestier tempéré 533
Jean-Jacques GEOFFROY & Marie-Louise CÉLÉRIER

Source : MNHN, Paris

Traces de l'activité de diplopodes dans des sols et des sédiments karstiques du Maroc atlantique 555
Colette JEANSON, Hsaïn EL AISSAOUI & Jean-Pierre ADOLPHE

Feeding rates and nutrient assimilation in the millipede *Jonespeltis splendidus* (Diplopoda, Paradoxosomatidae) 561
Kubra BANO

Sexual selection in savanna millipedes: products, patterns and processes 565
Steven R. TELFORD & John Mark DANGERFIELD

Trophic preferences of three soil macroarthropods (preliminary study) 577
Jorge P. CANCELA DA FONSECA & Leïla MEZIANE

Ecology and behaviour of *Xanthodesmus physkon* (Attems 1898), an aggregating paradoxosomatid from tropical West Africa 585
Dieter MAHSBERG

Déplacements en masse dans le sud-est de la France chez *Ommatoiulus sabulosus* (Myriapoda, Diplopoda, Julidae) avec invasions d'habitations 587
François SAHLI

COMMUNITIES IN ECOSYSTEMS

Distribution patterns and qualitative composition of the centipede fauna in forestal habitats of mainland Greece 599
Marzio ZAPPAROLI

On abundance, phenology and natural history of Symphyla from a mixedwater inundation forest in Central Amazonia, Brazil 607
Joachim ADIS, José Wellington DE MORAIS & Ulf SCHELLER

The ecology of savanna millipedes in Southern Africa 617
John Mark DANGERFIELD & Steven R. TELFORD

The diplopod community of a mediterranean oak forest in Southern France: ecological and evolutionary interest 627
Jean-François DAVID

Centipedes (Chilopoda) of some forest communities in Slovenia 635
Ivan KOS

Changes in the millipede (Diplopoda) community during secondary succession from a wheat field to a beechwood on limestone 647
Stefan SCHEU

Centipedes from Italian agroecosystems and their possible value as pest control agents 657
Marzio ZAPPAROLI

AUTHOR INDEX / INDEX DES AUTEURS 663

SYSTEMATIC INDEX / INDEX SYSTÉMATIQUE 665

Source : MNHN, Paris

Introduction

Jean-Jacques GEOFFROY

CNRS, Muséum National d'Histoire Naturelle, Laboratoire d'Écologie Générale. F-91800 Brunoy, France

Some twenty-seven years ago, a group of zoologists and biologists working on Myriapoda met in Paris (France) for the first time. 1968 was the birth year of international congresses of myriapodology and time when the Centre International de Myriapodologie took form. The creation of the CIM was the work of three people : J. M. DEMANGE (Paris), J. P. MAURIÈS (Paris) and O. KRAUS (Hamburg). Four years later, at Manchester, U.K. (1972), J. G. BLOWER joined the initial trinity as the fourth CIM Father, when organizing the Second International Congress of Myriapodology. These four men are the musketeers of the CIM. Ever since, a new congress has been organized through out the world every three years : Hamburg, Germany, 1975 (O. KRAUS), Gargagno, Italy, 1978 (M. CAMATINI), Radford, USA, 1981 (R. L. HOFFMAN), Amsterdam, The Netherlands, 1984 (C. A. W. JEEKEL), Vittorio Veneto, Italy, 1987 (A. MINELLI) and Innsbruck, Austria, 1990 (E. MEYER & K. THALER).

Some five years ago, according to previous formal sessions of the CIM, it was suggested that France, as first host-country and location of the permanent secretariat, should host the Ninth International Congress of Myriapodology in 1993. This date appeared to be a very significant one, as it saw the 25th anniversary of the CIM (1968-1993) and the bicentenary of the Muséum National d'Histoire Naturelle de Paris (1793-1993). We fully agreed with this idea, and decided to prepare a proposal wich was submitted to the plenary session of the CIM held in Innsbruck, Austria in July 1990. Paris was obviously the most appropriate place in France, due to the souvenir of famous zoologists and myriapodologists, the availibility of convenient facilities, the assistance of laboratories in the Muséum National d'Histoire Naturelle (MNHN), the Centre National de la Recherche Scientifique (CNRS) and the Université Pierre et Marie Curie (UPMC), the touristic interest of the city and the surroundings of the wide Fontainebleau forest...

In accordance with the discussions at Innsbruck, we decided to fix the period of the Congress to the end of July ; we also considered the possibility to organize some visits in National Galleries, an exhibition devoted to the activity of scientists durind the French Revolution, and a one-day excursion in various cultural and natural sites in the Fontainebleau area. Besides, we kept in mind to leave the scope of the Congress widely open to several topics, in order to contribute, by lectures and posters, to an up-to-date and more or less comprehensive knowledge about the biology of Diplopoda, Pauropoda, Symphyla, Chilopoda and - as is traditional - Onychophora. Our favorite creatures would appear as models for fundamental and applied biology and the contents of this volume plan to summarize this reality in 8 chapters :

GEOFFROY, J. J., 1996. — Introduction. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 13-17. Paris ISBN : 2-85653-502-X.

BIBL. DU MUSÉUM PARIS

Source : MNHN, Paris

Historical Myriapodology; Advances in Systematics and Biodiversity; Systematics and Evolution: Phylogenetic Relationships; Community Studies and Biogeography; Reproductive Developmental Trends; Physiology, Ecophysiology and Cell Biology; Population Biology, Soil Ecology and Behaviour; Communities in Ecosystems.

FIG. 1. — A logo for the CIM (Centre International de Myriapodologie : Secrétariat Permanent, MNHN Paris, 61 rue Buffon F-75231 Paris Cedex 05, France). Conceiving : GEOFFROY, MAURIÈS & NGUYEN DUY - JACQUEMIN. Drawn by Jacques REBIÈRE (MNHN).

Following the decision of the Centre International de Myriapodologie, an organization committee was soon established in France and through out the world.

Organizers: J. J. GEOFFROY (CNRS, MNHN, Brunoy), J. P. MAURIÈS (MNHN, Paris), M. NGUYEN DUY - JACQUEMIN (CNRS, MNHN, Paris), M. L. CÉLÉRIER (UPMC, Paris).

President of the Congress: J. M. DEMANGE (MNHN, Paris).

Organizing Committee: J. F. DAVID (CNRS, MNHN, Brunoy), M. DESCAMPS (USTL, Lille I), C. JAMAULT-NAVARRO (Université, Amiens), F. SAHLI (MNHN, Paris).

International Scientific Committee: J. ADIS (Plön, Germany), C.S. CRAWFORD (Albuquerque, USA), W. DOHLE (Berlin, Germany), W. DUNGER (Görlitz, Germany), H. ENGHOFF (Copenhagen, Denmark), S. I. GOLOVATCH (Moscow, Russia), W. B. JEDRYCZKOWSKI (Warsawa, Poland), C. A. W. JEEKEL (Amsterdam, The Netherlands), P. M. JOHNS (Christchurch, New-Zealand), O. KRAUS (Hamburg, Germany), J. G. E. LEWIS (Taunton, Somerset, U.K.), B. MEIDELL (Bergen, Norway), A. MINELLI (Padova, Italy), E. MEYER (Innsbruck, Austria), H. RUHBERG (Hamburg, Germany), U. SCHELLER (Järpas, Sweden), W. A. SHEAR (Hampden-Sydney, USA), R. M. SHELLEY (Raleigh, USA), B. R. STRIGANOVA (Moscow, Russia) and M. R. WARBURG (Haifa, Israel).

Source : MNHN, Paris

The Ninth International Congress of Myriapodology was held from 26-31, July 1993 at the Université Pierre et Marie Curie, PARIS VI and at the Muséum National d'Histoire Naturelle de Paris. A total of 129 members from 37 countries contributed or attended the Congress. Sessions were conducted over a five-day period with a mid-excursion to the Fontainebleau forest, castle and rocky sites. Numerous attendees visited the future Evolutionary Gallery and Micro-Zoo at the National Museum.

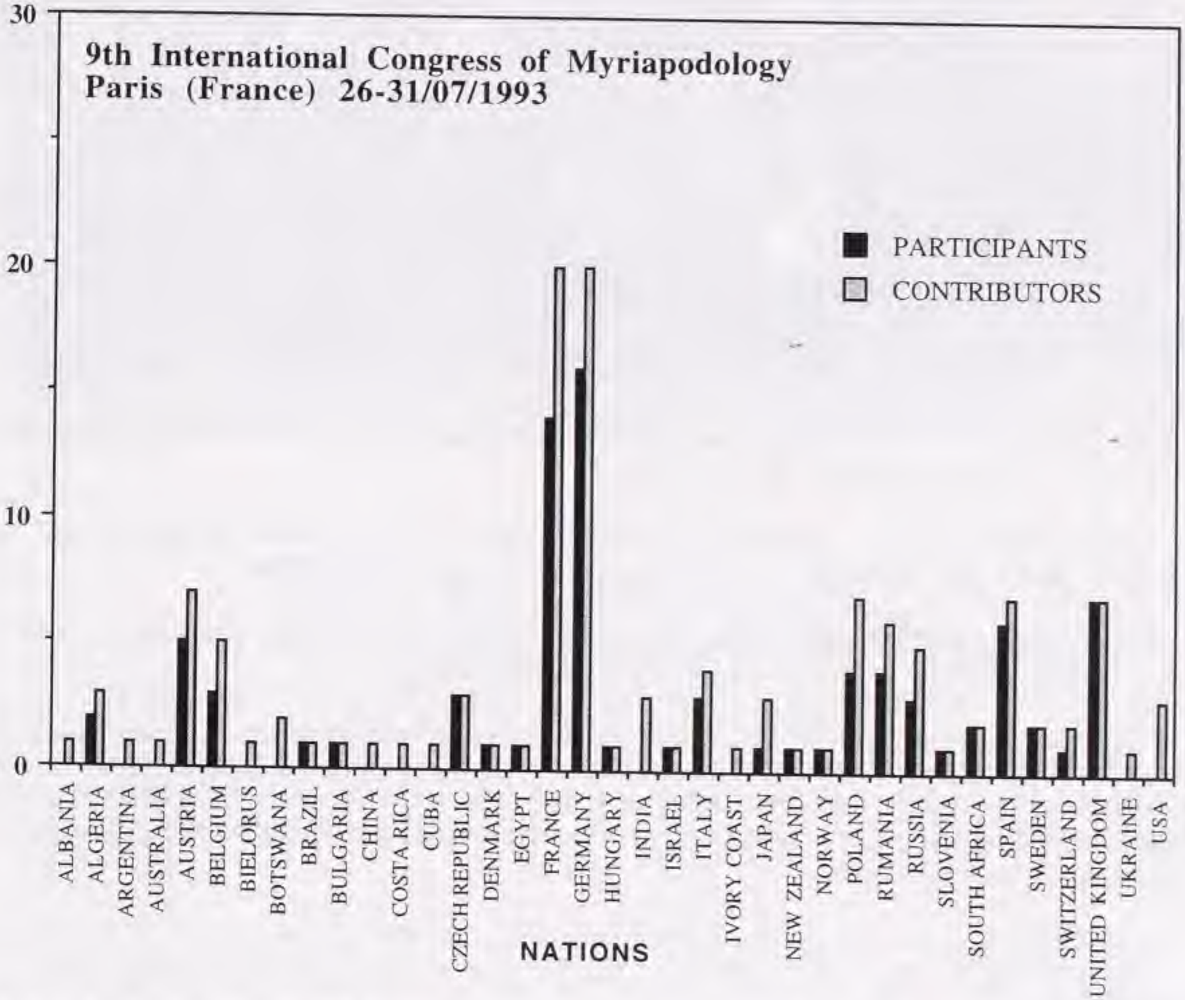


FIG. 2. — International participation to the 9th International Congress of Myriapodology (Paris, France, July, 1993).

There were 97 scientific contributions, by lectures or posters. 14 sessions topics represented the different themes. Seventy-nine papers were accepted for publication, some of them as short-papers or abstracts. This volume is based mainly on communications delivered during the 9th Congress but its main aim is to produce a recent up-to-date review of the biology (*s.l.*) of millipedes, centipedes, symphylids, pauropods, and onychophorans. It is meant for students of terrestrial arthropods and soil biology; as well as for researchers, biologists, zoologists, working in fields such as phylogeny, systematics, ecology, cell biology and others.

Source : MNHN, Paris

ACKNOWLEDGEMENTS

We gratefully acknowledge the financial support and practical assistance to the Congress provided by the different ministries, scientific institutions, societies and other bodies:

- Ministère des Affaires Etrangères (DDCSTE)
- Ministère de l'Enseignement Supérieur et de la Recherche (ACCES)
- Service le l'Information et de la Communication (UPMC, Paris VI)
- UFR Sciences de la Vie (UPMC, Paris VI)
- Parc Zoologique de Paris, Ménagerie du Jardin des Plantes (MNHN)
- Cellule de Préfiguration de la Galerie de l'Evolution (MNHN)
- Service des Relations Extérieures et Presse (MNHN)
- Service des Cultures (MNHN)
- Société de Biogéographie
- Société de Biospéologie
- Société Française d'Ecologie
- Calypso Log
- CAES du CNRS
- Office National des Forêts (ONF, Centre de Fontainebleau)
- RATP
- Société AGISSON

Special thanks to their efficient help to Esther CLÉMENT, Corinne GENOT, Gilles HORTAULT, Mark JUDSON, Chantal LARROCHE, Marie-Anne MONTANÉ, Dominique MORO, Anne ROUSSEL-VERSINI, Michèle BERTONCINI.

Many thanks to the CAES/CNRS for the exhibition on “French Scientists and the Revolution”, and to the SOCIÉTÉ AGISSON for manufacturing the Tee-shirts.

Congratulations and friendly thanks to Jacques REBIÈRE for both the pleasant and serious drawings, and to Valérie CHANSIGAUD for computer assistance.

A special mention must be adressed to the Laboratoire de Biologie & Physiologie des Organismes (UPMC, Prof. Y. TURQUIER), the Laboratoire d'Ecologie Générale (MNHN, Prof. P. BLANDIN) and the Laboratoire de Zoologie/Arthropodes (MNHN, Prof. Y. COINEAU) who provided logistic support during the Congress organization and during the busy exciting period of preparing the present volume.

Myriapodology moves on! We sincerely hope that myriapodologists (*s.l.*) will meet again numerous and in good spirits in Copenhagen in 1996, for a new fascinating rendez-vous with myriapod biology.

Paris, July 1995
Jean-Jacques GEOFFROY

Source : MNHN, Paris

FIG. 3. — During the Ninth International Congress of Myriapodology, Paris, July, 1993 : 1. F. Minelli; 2. F. Minelli; 3. S. Negrea; 4. C.-C. Prunescu; 5. T. Ceuca; 6. A. Serra; 7. J.-M. Demange; 8. J.-J. Geoffroy; 9. M. C. Vicente; 10. R. Bouzerna; 11. M.C. Miquel; 12. K. Tajovsky; 13. B. Striganova; 14. J. Wytwer; 15. E. Branquart; 16. M. Kos; 17. P. Johns; 18. O. Abrous-Kherbouche; 19. A. Schileyko; 20. M.-L. Célérier; 21. M. Warburg; 22. Z. Korsos; 23. G. Kania; 24. H. Read; 25. M. Kraus; 26. W. Dunger; 27. K. Voigtländer; 28. N. Bouzerna; 29. D. Mashberg; 30. J. Spelda; 31. M. Lesniewska; 32. Z. Korsos; 33. S.R. Telford; 34. M.P. Minelli; 35 M. Barnett; 36. A. Minelli; 37. S.P. Hopkin; 38. G. Ribarov; 39. E. Krabbe; 40. M. Nguyen Duy-Jacquemin; 41. J.-F. David; 42. R.D. Kime; 43. J.W. de Morais; 44. E. Christian; 45. B. Meidell; 46. F.J. Santibanez; 47. F. Weyda; 48. A. Pedroli-Christen; 49. V. Sustr; 50. G. Pass; 51. B. Condé; 52. H. Borucki; 53. H. Fründ; 54. K. Ishii; 55. O. Kraus; 56. I. Kos; 57. U. Scheller; 58. J. Adis; 59. A. Mette; 60. H. Ruhberg; 61. E. Robson; 62. P. Réveillet; 63. E. Meyer; 64. M. Di Giovanni; 65. M. Zapparoli; 66. L. Nevermann; 67. J.G.E. Lewis; 68. E.H. Eason; 69. S.I. Golovatch; 70. J.-P. Mauriès; 71. J. Rosenberg; 72. B. Rosenberg; 73. W. Dohle; 74. K.P. Zulka; 75. A. Tadler; 76. R.E. Jones; 77. H. Enghoff; 78. M. Descamps; 79. A.D. Barber; 80. P. Compere; 81. W. Jedryczkowski; 82. J.P. Cancela da Fonseca; 83. K. Jedryczkowski; 84. G. Andersson.

Source : MNHN, Paris

Source : MNHN, Paris

List of the Participants and Contributors

ALBANIA
QIRJO M.

ALGERIA
ABROUS-KERBOUCHE O.
BOUZERNA N.
DAAS T.

ARGENTINA
PEREIRA L. A.

AUSTRALIA
MESIBOV R.

AUSTRIA
CHRISTIAN E.
FISCHER E.
MARSONER P.
MEYER E.
PASS G.
TADLER A.
ZULKA K. P.

BELGIUM
BRANQUART E.
COMPÈRE P.
DEFISE S.
GASPAR C.
GOFFINET G.
KIME R. D.

BIELORUS
TARASEVICH Y.

BOTSWANA
DANGERFIELD J. M.
KAUNDA S.K.

BRAZIL
DE MORAIS J. W.

BULGARIA
RIBAROV G.

CHINA
WANG D.

COSTA RICA
MONGE-NAJERA J.
BARRIENTOS Z.
AGUILAR F.

CUBA
PEREZ-ASSO A. R.

CZECH REPUBLIC
SUSTR V.
TAJOVSKY K.
WEYDA F.

DENMARK
ENGHOFF H.

EGYPT
GHABBOUR S.

FRANCE
ADOLPHE J. P.
CANCELA DA FONSECA J. P.
CÉLÉRIER M. L.
CONDÉ B.
DAVID J. F.
DEMANGE J. M.
DESCAMPS M.
EL AISSAOUI H.
FABRE M. C.
GEOFFROY J. J.
GERARD S.
JAMAULT-NAVARRO C.
JEANSON C.
MAURIÈS J. P.
MEZIANE L.
NGUYEN DUY - JACQUEMIN M.
REVAULT P.
REVEILLET P.
SAHLI F.
VANNIER G.

GERMANY
ADIS J.
BORUCKI H.
DOHLE W.
DUNGER W.
EMMERLING C.
FRÜND H.
GREVEN H.
HAMANN S.
KRABBE E.
KRAUS M.
KRAUS O.
MAHSBERG D.
MARTENS J.
NEVERMANN L.
ROSENBERG J.
RUHBERG H.
SCHEU S.
SPELDA J.
VOIGTLÄNDER K.
XYLANDER W. E. R.

HUNGARY
KORSOS Z.

INDIA
BANO K.
PANDEY M. K.
TRIPATHI S. P.

ISRAËL
WARBURG M.

ITALY
DI GIOVANNI M.
MINELLI A.
NEGRISOLO E.
ZAPPAROLI M.
FUSCO G.

IVORY COAST
BOURDANNE KADEBE D.

JAPAN
ISHII K.
SHINOHARA K.
TAMURA H.

NEW-ZEALAND
JOHNS P.

NORWAY
MEIDELL B.

POLAND
ANDREJKO M.
JAROSZ J.
JEDRYCZKOWSKI W. B.
KANIA G.
LESNIEWSKA M.
STEFANIAK M.
WYTWER J.

ROMANIA
CEUCA T.
MATIC Z.
NEGREA S.
PRUNESCU C. C.
PRUNESCU P.
TABACARU I.

RUSSIA
GOLOVATCH S. I.
MIKHALJOVA E. V.
SCHILEYKO A. A.
STRIGANOVA B. R.
ZALESSKAJA N. T.

SLOVENIA
KOS I.

SOUTH AFRICA
BARNETT M.
TELFORD S. R.

SPAIN
DOMINGUEZ RODRIGUEZ M. T.
GARCIA RUIZ A.
MATEOS E.
MIQUEL M. C.
SANTIBAÑEZ F. J.
SERRA A.
VICENTE M. C.

SWEDEN
ANDERSSON G.
SCHELLER U.

SWITZERLAND
PEDROLI-CHRISTEN A.
SCHOLL A.

UKRAINE
CHORNYI N. G.

UNITED KINGDOM
BARBER A. D.
EASON E.
HILL T.J.
HOPKIN S. P.
JONES R. E.
LEWIS J. G. E.
READ H.
ROBSON E.
WAKLEY G. E.

USA
CRAWFORD C. S.
EDGAR G. A.
MULVEY M.

Source : MNHN, Paris

Source : MNHN, Paris

Allocution d'ouverture

Jean-Marie DEMANGE

Président du IXème Congrès International de Myriapodologie (MNHN - Zoologie, Arthropodes - Paris)

M. le Président, M. le Directeur, mes chers Collègues, Mesdames, Messieurs.

Le plaisir que nous éprouvons, celui de se trouver tous réunis, nous le devons à ceux qui nous ont aidés, soit matériellement, soit financièrement. Je tiens à remercier tout particulièrement tous ceux grâce à qui nous sommes là aujourd'hui : tout d'abord l'Université Pierre et Marie Curie en la personne du Professeur J. LEMERLE, Vice Président, son représentant ; non seulement pour son aide financière mais aussi pour tous les moyens mis à notre disposition, ne serait-ce que cet amphithéâtre et tout le matériel y afférent. Je remercie également le Professeur J. GUERDOUX, directeur de l'UFR Sciences de la Vie pour sa généreuse participation financière. C'est grâce aux efforts du Professeur Y. TURQUIER notamment et de notre collègue Madame Marie-Louise CÉLÉRIER que furent élaborées les affiches du Congrès, le fascicule des résumés des communications, les panneaux, etc. M. L. CÉLÉRIER a assuré, en outre, la liaison entre notre Laboratoire du Muséum et l'Université. Le Muséum National d'Histoire Naturelle, actuellement en pleine rénovation (Grande Galerie de l'Evolution, Amphithéâtres, Bibliothèque...) a mis à notre disposition la logistique de deux de ses laboratoires et accueille plusieurs évènements de notre congrès. De plus, une aide financière assez importante a été débloquée à notre profit pour que tout se passe bien. Je remercie Monsieur le Professeur Jacques FABRIÈS, Directeur du Muséum , pour cette généreuse contribution.

Vous avez bien voulu également accepter, Monsieur le Directeur, que notre réunion amicale d'accueil se tienne à la *Rotonde* de la Ménagerie du Jardin des Plantes, ce qui est exceptionnel. A cette occasion, j'adresse au Professeur Jean-Jacques PETTER, Directeur de la Ménagerie du Jardin des Plantes et de la Conservation des espèces animales (Zoo), ma plus vive reconnaissance. La Rotonde est un monument magnifique, récemment restauré, construit de 1804 à 1812, en forme de Croix de la Légion d'Honneur dont l'ordre était créé par Napoléon 1er deux ans auparavant. Elle abrita, pendant près de vingt ans, la célèbre girafe offerte au Roi Charles X par Mehemet Ali, Pacha d'Egypte. Cette Rotonde était au départ destinée à présenter les “animaux féroces” mais ce furent plutôt les “animaux paisibles” qui l'occupèrent. Elle est aujourd'hui le temple des arthropodes, des microarthropodes notamment, dont l'exposition et les appareils d'observation uniques qui la composent ont été créés par le Professeur Yves COINEAU

DEMANGE, J.-M., 1996. — Allocution d'ouverture. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 21-23. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

et expérimentés au Parc Zoologique du Bois de Vincennes... les gros animaux et les tout petits... "de la Puce à l'Eléphant"...

Nos collègues japonais auront, sans doute, été surpris et intrigués de trouver au milieu du petit temple qui forme la partie centrale du bâtiment, une magnifique sculpture représentant une japonaise. Ne voyez aucun message dans la présence de cette statue ; elle est superbe, en albâtre et comme un temple a toujours sa statue...... Cette statue a une histoire et si cette japonaise paraît un peu fantaisiste aux yeux de nos collègues, qu'ils voient en cette oeuvre l'inspiration d'un artiste. C'est une figure allégorique représentant le Japon, l'un des Pays participants de l'Exposition Universelle de 1878. Elle est l'œuvre d'un artiste français Eugène AIZELIN et ceci explique cela. Je remercie donc également, à un double titre, le Professeur Yves COINEAU : en tant que responsable scientifique, créateur de cette exposition et en tant que Directeur du Laboratoire de Zoologie/Arthropodes du Muséum ; il a bien voulu nous apporter, en outre, une aide précieuse et efficace pour la bonne réalisation de notre Congrès. Notre collègue le Professeur Patrick BLANDIN a largement pris en charge, au Laboratoire d'Ecologie Générale, toutes sortes de frais divers très lourds pour notre petite communauté. N'oublions pas, enfin, le Ministère des Affaires étrangères, qui apporta sa contribution par son bureau des Congrès, en débloquant une forte somme et le Ministère de la Recherche qui y ajouta sa contribution financière. Le CAES du CNRS, quant a lui, nous a confié les panneaux de son exposition traitant "des *Savants et la Révolution*" qui sont présentés dans le hall. Tout cela fait donc que nous sommes là aujourd'hui, mais l'argent n'est pas tout. N'oublions pas mes collègues du Comité d'Organisation qui se sont dépensés sans compter, je dirais même dévoués pour aplanir toutes les difficultés et Dieu sait qu'il y en eut ! et organiser de main de maître cette rencontre.

Notre infatigable et dynamique collègue Jean-Jacques GEOFFROY fut un moteur très efficace épaulé en cela par Monique NGUYEN DUY - JACQUEMIN et Jean-Paul MAURIÈS. Beaucoup d'autres nous ont aidé et beaucoup nous aiderons encore pendant nos réunions, je veux parler de toutes les personnes de l'Université et du Muséum, de tous les niveaux. Merci, merci encore à tous et pour tout.

Je voudrais dire combien je suis sensible à l'honneur qui m'est fait d'avoir été nommé à la Présidence de ce Congrès. Je veux voir dans cette distinction un témoignage de sympathie, d'amitié et j'en suis d'autant plus touché. Ce signe de l'amitié n'est il pas exprimé d'ailleurs parfaitement dans le logo qui marque notre Congrès? C'est même le signe de l'union qui a toujours été celui du CIM (Centre International de Myriapodologie), que l'on peut reconnaître dans ce couple de Mille-Pattes enlacés qui reproduisent la tour Eiffel. Il y a 25 ans, nous nous rencontrions à Paris pour la première fois dans le cadre du 1er Congrès international de Myriapodologie. C'est en son sein que fut créé le CIM , par trois d'entre nous: le Professeur Otto KRAUS, ici présent, alors à Francfort, Jean-Paul MAURIÈS du Laboratoire des Arthropodes et moi-même. En ce quart de siècle d'existence, plusieurs de nos collègues, présents à Paris en 1968, nous ont quittés : Mrs. Nell Bevel CAUSEY, Ulrich HAACKER qui anima si parfaitement et si brillamment nos séances en se proposant spontanément "traducteur simultané" par sa connaissance des langues et sa valeur scientifique, le Professeur Robert JOLY, des Universités de Lille et d'Amiens, spécialiste de l'endocrinologie de *Lithobius forficatus* et des phénomènes de mue, le Dr. Karl STRASSER l'un de nos doyens avec le Révérend Cannon BRADE-BIRKS et enfin, plus récemment, le Professeur Max VACHON, ancien directeur du Laboratoire de Zoologie des Arthropodes. J'ai, par ailleurs, voulu évoquer la mémoire de tous les myriapodologistes disparus, dans une sorte de préface au recueil des résumés des communications car je souhaite qu'ils soient présents à nos côtés. Ne les oublions pas en un jour comme celui-ci. [A l'heure où paraîssent ces lignes, un autre de nos fidèles nous a quitté, en 1994 : Colin Peter FAIRHURST]. Les uns nous quittent mais d'autres nous rejoignent et nous voyons aujourd'hui beaucoup d'entre eux, de la nouvelle génération de chercheurs, qui viennent enrichir notre communauté.

Parti de Paris, notre mouvement revient à Paris après avoir parcouru le Monde; successivement Manchester, Hambourg, Gargnano, Radford, Amsterdam, Vittorio Veneto et

Source : MNHN, Paris

Innsbruck enfin, en 1990. Depuis 1968, le nombre des Pays participants ne cesse d'augmenter: de 13 à Paris, il y en eût 25 à Innsbruck et aujourd'hui 37. Je suis heureux de souhaiter particulièrement la bienvenue à ces nouveaux représentants.

Cette année 1993 revêt une solennité toute particulière, non seulement parce que c'est un retour aux sources mais surtout par deux symboles : - le bicentenaire de la création de notre grande et vénérable Maison qui de *Jardin du Roi* devient *Muséum d'Histoire Naturelle* par décret de la Convention du 10 juin 1793 ; - la venue officielle au Muséum, à cette même date, de Jean Baptiste Pierre Antoine de Monet, chevalier de LAMARCK, l'un des trois artisans de la création de notre Etablissement avec BUFFON et DAUBENTON. Ce dernier symbole revêt, pour nous chercheurs du Laboratoire de Zoologie/Arthropodes, une importance particulière en ce que notre laboratoire est l'un des descendants directs de la chaire confiée à LAMARCK. Elle fut divisée, en 1830, en deux chaires : "*Crustacés et Insectes*" confiée à Pierre André LATREILLE et "*Annélides, Mollusques et Zoophytes*" confiée à Henri Ducrotay de BLAINVILLE. Une troisième chaire en fut détachée en 1917: "*Vers et Crustacés*", de laquelle est issue, plus récemment (1960) celle de "*Zoologie/Arthropodes*". Le Laboratoire de "*Zoologie/Arthropodes*" conserve les collections d'origine de crustacés, arachnides, myriapodes, augmentées de collections célèbres dont celles de Henri Wilfrid BRÖLEMANN et Henri RIBAUT, pour ne parler que des myriapodes. En ce qui concerne Henri-Wilfrid BRÖLEMANN, qu'il me soit permis d'évoquer brièvement sa mémoire car il est incontestablement le père de la Myriapodologie en France. Né le 10 juillet 1860, il est décédé le 31 juillet 1933. Appartenant à une famille de grands industriels et de banquiers, banquier lui-même, il s'intéresse très tôt aux myriapodes et finit par abandonner son métier d'origine pour se consacrer totalement à l'étude des "Mille-pattes". Spécialiste de réputation internationale incontestée, il publie 160 travaux plus particulièrement consacrés aux diplopodes. C'était un homme de grande culture, un érudit... Il est l'auteur d'une théorie évolutive, pour les myriapodes, basée sur un "principe de contraction" où il considère une évolution du groupe vers une réduction du nombre des segments par arrêt de développement. Ce principe de contraction s'oppose à un "principe d'élongation" soutenu, à l'inverse, par Karl Wilhelm VERHOEFF, spécialiste allemand. Mais le temps des fondateurs est révolu, du point de vue de notre spécialité, la myriapodologie, nous nous retrouvons aujourd'hui très nombreux et l'on a pu apprécier, au cours de nos réunions successives la montée de la jeune génération. On peut donc envisager l'avenir avec confiance et souligner que la systématique est toujours à l'ordre du jour, bien vivante et dynamique à une époque où le concept de biodiversité s'impose. Le programme de ces journées est chargé, très chargé, abordant tous les sujets de la molécule à la pure systématique ; mettons nous vite au travail et pour cela je déclare ouvert le 9ème Congrès International de Myriapodologie de Paris.

Source : MNHN, Paris

Source : MNHN, Paris

Myriapodology before and after Martin Lister's «*Journey to Paris in the Year 1698*»

Stephen P. HOPKIN

School of Animal and Microbial Sciences, University of Reading, P.O. Box 228, Reading, RG6 2AJ, U. K.

ABSTRACT

The most famous publication of Martin LISTER (1638-1712) was his account of his «*Journey to Paris in the year 1698*». The book is well-known for its detailed descriptions of everyday life in France at the end of the 17th century. Of interest to myriapodologists, however, are the striking illustrations by Father Charles PLUMIER of two myriapods from Brazil, a millipede "*Iulus Americanus*" and a centipede "*Scolopendra Americana*". Indeed, myriapods have featured prominently in zoological literature since the time of Aristotle 384-322 BC. The development of myriapodology has mirrored the scientific revolution since the Renaissance. This paper gives an overview of the passage from folklore and whimsy, through the seminal observations of Leeuwenhoek, the "compendia" of 18th century zoologists including LINNAEUS, culminating with the flowering of scientific myriapodology in the 19th century.

RÉSUMÉ

La myriapodologie avant et après le «*Voyage à Paris en l'an 1698*» de Martin LISTER.

La plus célèbre publication de Martin LISTER (1638-1712) fut sa relation de son «*Voyage à Paris en l'an 1698*». Le livre est surtout connu pour sa description détaillée de la vie quotidienne des français à la fin du 17ème siècle. Il présente cependant un intérêt pour les myriapodologistes, à travers les illustrations saisissantes, dues au Père Charles PLUMIER, de deux myriapodes du Brésil, un diplopode, "*Iulus Americanus*" et un chilopode, "*Scolopendra Americana*". Les myriapodes ont vraiment été éminemment représentés dans la littérature zoologique depuis l'époque d'Aristote (384-322 BC). Le développement ultérieur de la myriapodologie a reflété la révolution scientifique qui s'est opérée depuis la Renaissance. Ce travail se propose de passer en revue cette évolution qui, depuis le folklore et la fantaisie, à travers les observations de Leeuwenhoek, grâce aux précis et traités des zoologistes du 18ème siècle - parmi lesquels figure LINNÉ -, a abouti au développement considérable de la myriapodologie qui a fleuri au 19ème siècle.

INTRODUCTION

"It is a noble employment to rescue from oblivion
those who deserve to be remembered"
Pliny the Younger, Letters V.

Centipedes and millipedes are among the most prominent of terrestrial invertebrates. It should not surprise us to find numerous references to myriapods throughout the literature of the past. However, the modern approach to research emphasises topicality. Work rapidly becomes "out of date". Few scientists have the time to study the books and papers of their predecessors from previous decades, let alone earlier centuries.

HOPKIN, S. P., 1996. — Myriapodology before and after Martin Lister's «*Journey to Paris in the Year 1698*». *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 25-34. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

During the latter stages of research for "*Biology of Millipedes*" (HOPKIN & READ, 1992), I began to uncover references to myriapods dating back as far as the 15th century. These discoveries were made too late to include in our book. However, since then I have tracked down more than 50 references to centipedes and millipedes in pre-19th century literature, many illustrated with exquisite woodcuts, engravings and drawings, some in colour.

In this article, I shall give an overview of the development of myriapodology from the time of Aristotle (384-322 BC) to the mid-19th century. Before Martin LISTER's journey to Paris in 1698, most observations on myriapods were apocryphal, or related to medicines. In the late 17th century, and 18th century, the diversity of invertebrate life began to be appreciated. Numerous "compendia" were published, the most important of which was the 10th edition of the *Systema Naturae* of LINNAEUS (1758) which formed the basis of modern nomenclature.

The 19th century saw the application of scientific method to the study of centipedes and millipedes and eventually symphylids and pauropods, although these two groups are not covered here. This was the "Golden Age" of myriapodology. The beauty and accuracy of publications by VON STEIN (1841), WAGNER (1841), NEWPORT (1843), SWAN (1864), and the magnificent coloured plates of KOCH (1863), are testimony of the high standards that can be achieved from long and careful observation with simple equipment. These workers laid the foundations of modern myriapodology and we shall forever be in their debt.

THE DAWN OF MYRIAPODOLOGY

The earliest student of zoology whose work has survived was ARISTOTLE (384-322 BC). Several references to myriapods can be found in translations of his work (e.g. THOMPSON, 1910). In one section on "insects", millipedes and centipedes are recognised as different organisms - "some insects are wingless such as the *Iulus* and the centipede". Elsewhere, the distinction between the "Sea Scolopendra" polychaete worm and "Land Scolopendra" is made, the source of much confusion in later centuries. The comment is made that if a *Scolopendra* is cut in half, the two pieces move off in opposite directions!

PLINY THE ELDER (AD 23-79) brought together earlier bodies of scientific knowledge, most notably in his 37-volume *Naturalis Historia* (FORD, 1992). Translations of Pliny's work (e.g. HOLLAND, 1601) include several references to "multipedes". However, there is confusion as to whether these are centipedes, millipedes or woodlice (terrestrial Isopoda). A description of a cure for "biting of the cheeselips or many feet worms called multipedes" could refer to either.

There is one other pre-Renaissance reference to myriapods in the form of a small woodcut of a "Skolopendra" (Fig. 1) made by a Byzantine artist in AD 512 to illustrate the Greek Herbal compiled in the first century AD. by DIOSCORIDES (GUNTHER, 1934). "Skolopendra" are included due to their supposed medicinal properties. However here, as on numerous other occasions, it is impossible to decide whether centipedes, or marine polychaete worms, are being discussed.

FIG. 1. — Illustration by a Byzantine artist in AD 512 to illustrate the Greek Herbal of DIOSCORIDES (from GUNTHER, 1934).

Source : MNHN, Paris

The real dawn of zoology after the "dark" period of the Middle Ages is connected with the name of an Englishman, Edward WOTTON, born at Oxford in 1492, who practised as a physician in London and died in 1555. WOTTON's *De Differentiis Animalium* (1552) moved away from the mythological creatures of earlier works and towards more factual descriptions.

The earliest unambiguous illustrations of marine polychaete worms appeared in the *Libri de Piscibus Marinis* of RONDELETIUS (1507-1566) published in 1554. The woodcuts of "Sea Scolopendra" included in this important book reappear many times in later centuries and are frequently mis-identified as centipedes.

The first definite illustration of a centipede occurs in the herbal of MATTHIOLUS (1500-1577) published in 1569. The good sale of his smaller herbal in 1554 with small woodcuts caused MATTHIOLUS to prepare a luxurious edition. Ferdinand I whose physician ordinary Matthiolus was made a large contribution towards the cost. The fine woodcuts were done by Giorgio LIBERALE and Wolf MEIERPECK and the blocks were first printed in the German edition printed at Prague in 1563, and then sent to Venice. The illustrations of "Sea Scolopendra" were copied and cited as such from RONDELETIUS (1554). However, there is an original woodcut of a *"Scolopendra"* which is a true centipede (Fig. 2). The animal is clearly drawn from a specimen rather than from memory.

FIG. 2. — A "*Scolopendra*" from MATTHIOLUS (1569).

ALDROVANDI (1522-1605) in *De Animalibus Insectis* (1638) distinguishes between millipedes "*Iulus*", centipedes "*Scolopendra terrestris*" and polychaete worms "*Scolopendra marina*", but unfortunately, the accompanying illustrations of what are clearly *Lithobius*, have 11 or 14 pairs of legs instead of the correct 15 pairs. Indeed, the presence of the correct number of legs on a myriapod as in the illustration of a Brazilian centipede in PISO (1658), is a good guide to the scientific accuracy of the artist.

The writings of WOTTON (1552), and Conrad GESNER (1516-1565) in his huge five-volume *Historia Animalium* (1551, 1558, 1587, 1617), were summarised and illustrated by Thomas MOUFET sometimes MOUFFET, MUFFET or MOFFETT (1553-1604). MOUFET, a contemporary of SHAKESPEARE, studied medicine at Cambridge and Basel, and practised at Ipswich and London. His *Insectorum sive Minimorum Animalium Theatrum* (1634) contains several woodcuts of recognisable myriapods including a *Lithobius* with the correct number of legs (15 pairs), and a rather fine millipede on the title page (Fig. 3). Some editions contain an Appendix of four plates which are rarely seen. On one of these is a copy of the woodcut of the "*Scolopendra*" of MATTHIOLUS (1569) which has "lost" a pair of legs during the copying!

An English version of the work of WOTTON, GESNER & MOUFET was published by Edward TOPSEL (1572-1628) in his *History of Four-footed Beasts and Serpents* (1658). TOPSEL's book contains several pages of delightful prose "concerning the Scolopendrae and

Source : MNHN, Paris

Juli". The Juli "the English after me will call them Gally-worms" - from the resemblance of the numerous legs to oars on a ship - are treated separately from the Scolopendrae, although polychaete worms are included with the latter judging from the accompanying illustrations. Both Scolopendrae and Juli are included with the "Cheeselips" (woodlice) as the "Many-feet", a persistent theme (see e.g. KIRCHER, 1678; SIBBALD, 1684; BRADLEY, 1721; HILL, 1752; SEBA, 1735). Topics mentioned include swarming, metachronal waves of the legs, and the use of myriapods as medicines, particularly for removal of unwanted hair! There are also references on the use of "many feet" as diuretics, a common theme in early medicinal texts (e.g. BOYLE, 1744; JAMES, 1743-1745). Some authors have even reported "multipeda" being excreted with the urine (PARÉ, 1634; ALDROVANDI, 1638).

INSECTORVM
SIVE
Minimorum Animalium
THEATRVM:
Olim ab
EDOARDO WOTTONO,
CONRADO GESNERO,
THOMAQVE PENNIO
inchoatum:
Tandem
THO. MOVFETI Londinâtis operâ sumptibusq; maximis concinnatum, auctum, perfectum:
Et ad vivum expressis Iconibus suprà quingentis illustratum.

Londini ex Officinâ typographicâ Thom. Cotes. 1634.

FIG. 3. — The title page of MOUFET (1634).

The following passages from TOPSEL (1658) describe the effects of centipede bites in vivid detail.

"This Scolopender being provoked bites so sharply that *Ludovicus Armarus* who gave me one brought out of Africa could scarce endure him to bite his hand, though he had a good glove on, and a double linen cloth; for he struck his forked mouth deep into the cloth, and hung on a long time, and would hardly be shaken off"

"When the land Scolopender hath bitten, the place is all black and blue, putrifies and swells, and looks like to the dregs of red wine, and is ulcerated with the first bite"

The *Historiae Naturalis* of JONSTONUS (1657a) and the English translation (1657b) are examples of the pitfalls of plagiarism although to be fair to JONSTONUS, he does cite the sources of his illustrations. Much of the text is based on earlier authors and many of the illustrations are copied from the work of ALDROVANDI, GESNER, MOUFET & TOPSEL. In addition to repeating the mistakes of earlier authors the 22 and 48 legged *Lithobius* of ALDROVANDI are reproduced,

Source : MNHN, Paris

JONSTONUS introduced errors during the copying. Some creatures have "lost" or "gained" legs. The small illustration of a woodlouse, for example, has seven pairs of legs in MOUFET & TOPSEL, but has gained two extra pairs in JONSTONUS's book. This "eighteen-legged woodlouse" still turns up from time to time, most recently in an advertisement for Robinson's Barley Water in the U.K. as part of a series on ancient remedies.

The mid to late 17th century was a period of transition. Work of supreme quality was published at the same time as anecdotal evidence for outdated concepts such as spontaneous generation. The illustrations in KIRCHER (1678) appear to suggest the development of a centipede from a putrifying horsetail plant *Equisetum* (Fig. 4). However, the invention of the microscope enabled Robert HOOKE (1635-1702), Jan SWAMMERDAM (1637-1680) and Anthony van LEEUWENHOEK (1632-1723) to publish some of the most important and original zoological observations ever made.

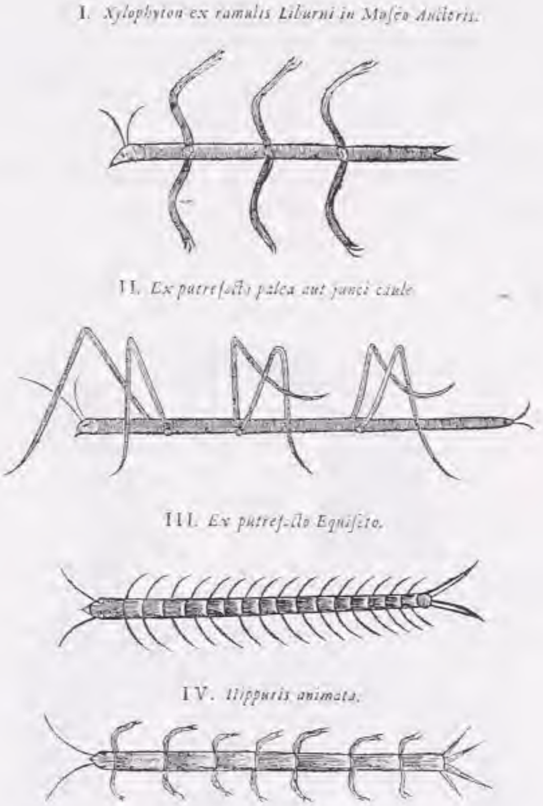


FIG. 4. — "Spontaneous generation" of animals from plants (from KIRCHER, 1678), including a centipede (III) developped from a putrified horsetail (*Equisetum*).

HOOKE's *Micrographia* (1665) does not concern us here as this classic work contains no reference to myriapods. The *Historia Insectorum Generalis* of SWAMMERDAM (1669), English translation (1758) again contains no illustrations of myriapods. However, in one passage, SWAMMERDAM does make some brief observations on myriapods remarking that he is in possession of "a *Scolopendra* of the largest kind which is even a span long and was sent to me from the East Indies". It is to LEEUWENHOEK's *Werken* (1684-1718) that we must turn for the first observations on myriapods displaying true application of scientific method.

LEEUWENHOEK discovered the aperture in the poison claws of centipedes (Fig. 5). In his "Letter 104" sent to the Royal Society on 17th October 1687 from Delft (English translation, 1964), LEEUWENHOEK wrote the following:

Source : MNHN, Paris

"I have often heard people speak about the poisonous nips or Bites, by a certain vermin, which is called Thousand-legs in the East Indies; this vermin as I was told comes to walk on the naked body of sleeping Persons, and as this vermin is very cold, People often become restless when they feel these animals. But if People would lie quietly without moving themselves, the same would not cause People any injury; but owing to this movement, they nip, with the pincers that they have in front of their head into People's bodies; and although there is no effusion of blood following this, and only a small red or blue spot remains where this vermin has nipped into the body, there nevertheless follows an intolerable pain and swelling, which is greater and lasts longer in one Person than in another. To still this pain there is, they say, no more effective remedy than to kill these Centipedes alive in the olive oil, and to rub this oil into the affected part. Last year I instructed the workmen in this city, who receive the goods from the East Indies, to bring me a live centipede, with the intention to discover, if possible, the reason for these harmful bites of the centipede. They thereupon brought me a Centipede the length of a little finger while some others are quite two fingers long and more. I took hold of this Centipede by one of the two pincers, with a small pair of pliers; and on bringing the pincer before the microscope, I saw that the pincers or nippers were continuously being moved towards and away from each other, to nip or grasp something; in which movement I observed at the same time that each of these pincers was provided with a tiny hole, which hole had a small groove or gutter, which was made in such a way as to bring the fluid that came oozing out of this hole to the extreme end of this sharp, sting-like pointed part with which the pincer is fitted.
From these observations, I came to suppose that the Centipede, by nipping with his pincers into People's skin used so much violence that he damaged some blood- and other vessels, and tore them apart, and that, at the same time, he injected the aforesaid fluid into the skin. And I furthermore supposed that this fluid was mixed with an injurious sharp Salt: and that it was not the damage done by the nipping that caused the great pain; but only the suffering inflicted by the noxious fluid.

I had intended to continue my observations this year, and to this end I had instructed the Workmen to catch the Centipedes. But they have not observed any, although several were seen on board ship during unloading of the goods, and were killed there."

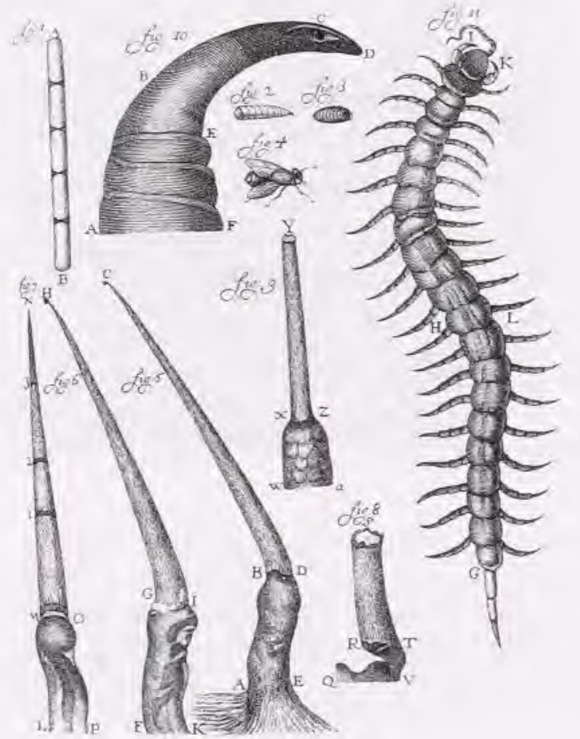


FIG. 5. — A plate from LEEUWENHOEK's *Werken* (1684-1718) sent to the Royal Society on 17th October 1687. "Fig. 10" shows the poison claw of a centipede ("Fig. 11") which has one of its anterior-most legs missing. The other illustrations are of the stings of nettle (*Urtica*).

The observation of LEEUWENHOEK on poison claws were referred to more than a century later by SMELLIE (1790-1799) in his discussion of the effects of centipede bites.

Source : MNHN, Paris

"The poisonous weapons of the *Scolopendra*, or *centipes*, are somewhat different from those of the spider. Its bite is so painful, especially in the East Indies, as we are informed by BONTIUS, that it makes the patient almost mad. When the claws of its forceps are examined by a microscope, on the upper side of each of them, near the point, a small aperture appears, through which the venom is conveyed to the wound. Of the East India centipedes, LEEUWENHOEK had one sent to him alive; and he found that by pressing the claw, a small drop of liquor issued out of this aperture".

LEEUWENHOEK was clearly a man ahead of his time.

MARTIN LISTER'S JOURNEY TO PARIS

Martin LISTER (1638-1712) was an English naturalist who published important books on spiders and snails; for a recent biography of LISTER, see PARKER & HARLEY (1992). In 1698, LISTER was sent by King William III as a medical attendant to William BENTINCK, Earl of Portland, on a diplomatic mission to Paris. He recorded his experiences in the one book he published in English, *A Journey to Paris in the year 1698*.

LISTER's account of his visit to Paris proved very popular and ran to three editions in his own lifetime. It contains much of historical interest and, in particular, its information about scientific, medical and other technical matters as well as its description of the city itself, and the 17th century way of life, are invaluable in their detail.

Included in the book are six folding plates. Two of these are among the most striking illustrations of myriapods ever published. Plate 5 (Fig. 6) shows a large millipede "*Iulus Americanus*" and Plate 6 (Fig. 7) a centipede "*Scolopendra Americana*", both drawn by Father Charles PLUMIER. The centipede was in PLUMIER's collection and was "a foot and a half long, and proportionally broad". LISTER describes seeing the millipede in the collection of Monsieur TOURNEFORT.

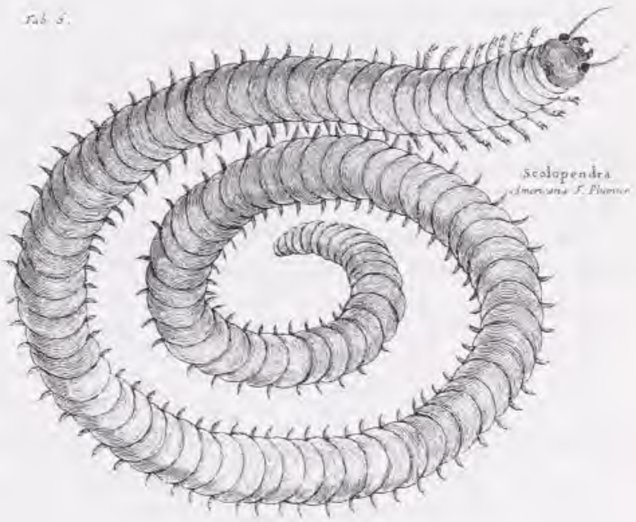


FIG. 6. — Left: "*Iulus Americanus*" drawn by Father Charles PLUMIER (from LISTER, 1699).
FIG. 7. — Right: "*Scolopendra americana*" drawn by Father Charles PLUMIER (from LISTER, 1699).

Source : MNHN, Paris

" He showed me a very great *Julus* from Brazil, at least six inches long, and two about, round like a cord, very smooth and shining, of a kind of copper or brazen colour: the feet infinite, like a double fringe on each side: this he had from F. PLUMIER, who afterwards gave me a design of it drawn by the life and in its proper colours".

For someone used to British myriapods, the sight of these spectacular creatures clearly had a lasting impression on Martin LISTER.

COLLECTION AND CLASSIFICATION

The 18th and early 19th centuries were periods when the huge diversity of animal life began to be appreciated and comprehensively described. The lavish texts of HILL (1752), SCHAEFFER (1766), BARBUT (1781), DONOVAN (1792-1807), GEOFFROY (1799), SHAW (1800-1826), CUVIER (1838-1849), OKEN (1833-1842) and BERNARD *et al.* (1842/1843) all contain illustrations of myriapods, many in colour. Huge collections of specimens were built up. The wealthy Dutchman Albert SEBA (1665-1736) assembled the richest collection of natural history objects of his time. His private museum contained several centipedes and millipedes which are described and illustrated in the catalogue SEBA (1734-1765). SEBA's specimens were purchased by Peter the Great and moved to St. Petersburg.

The most important development of the 18th century was the system of classification introduced by Carolus LINNAEUS (1707-1778) in the first edition of his *Systema Naturae* (1735). The tenth edition (1758) ranks as one of the most important zoological book ever published.

In the first edition of *Systema Naturae* (1735), LINNAEUS recognises five classes of animals. Class 5, the Insecta, is split into four groups namely Coleoptera, Angioptera, Hemiptera and Aptera. The Aptera contains eight "Genera" which are separated mainly on the basis of the number of legs. Woodlice Genus *Oniscus*, "Pedes 14" are distinguished from the myriapods which are all in the Genus *Scolopendria* "Pedes 20" or more. Three "species" are described, *Scolopendria terrestris*, *Scolopendria marina* (polychaete worm), and *Julus*.

LINNAEUS's introductory notes "Observationes in Regnum Animale". Observations on the Animal Kingdom were translated into English by ENGEL-LEDEBOER & ENGEL in the facsimile edition of 1964. Point 8 "Scintillas *Scolopendrae*" is translated as "the luminescence of *Scolopendria marina* a Nereide". However, it seems much more likely that LINNAEUS is referring to terrestrial species in which luminescence has been repeatedly observed (BARBUT, 1781; DONOVAN, 1792-1807; SHAW, 1800-1826).

The classification of myriapods is more detailed in the tenth edition of *Systema Naturae*, with the "Insecta" comprising seven groups, the last of which "Aptera" contains 14 "Genera" numbers 230-243. The centipedes (Genus 242 *Scolopendra* - nine species) are separated from the millipedes (Genus 243 *Julus* - seven species), although nereid polychaetes are still included as *Scolopendra marina*. The names of *Scolopendra electrica* from *elektron*, "a shining substance, amber or an alloy of gold and silver" (EMMET, 1991) and *Scolopendra phosphorea* clearly refer to properties of luminescence. Several of LINNAEUS's names are, of course, still in use today.

THE "GOLDEN AGE" OF MYRIAPODOLOGY

By the early 19th century, myriapods began to be recognised as a group distinct from insects. The catalogue of British insects published by STEPHENS (1829) does not include centipedes or millipedes. The *Nomenclator Zoologicus* of AGASSIZ (1842-1846) contains many genus and family names that are familiar to us today. The *Myriapodum* were divided into two groups: *Chilognatha*, the millipedes comprising the families Glomeridae, Julidae, Polydesmidae, Polyxenidae, Polyzonidae and Siphonophoridae and *Chilopoda*, the centipedes comprising the families Cermatidae, Lithobiidae, Scolopendridae and Geophilidae.

The internal anatomy of millipedes and centipedes began to be studied in detail from the mid 19th century onwards. The standard of draughtmanship of the plates in books by VON

Source : MNHN, Paris

STEIN (1841), WAGNER (1841), SWAN (1864), and the paper by NEWPORT (1843) has not been bettered since. However, the peak of myriapodological illustration must surely be *Die Myriapoden* by Carl Ludwig KOCH (1778-1857) published in 1863. This book contains descriptions of more than 200 species of centipedes and millipedes, each of which is figured in colour plates of breathtaking beauty. These paintings must rank among the most exquisite ever produced and are a fitting tribute to the efforts of earlier myriapodologists. KOCH's *Die Myriapoden* released from relative obscurity what are surely among the most interesting of the least-studied animals. Even NEWPORT (1841) bemoaned the preoccupation of naturalists with insects to the detriment of other arthropods.

ACKNOWLEDGEMENTS

I am very grateful to Mike BOTT, David KNOTT and Dermot O'ROURKE of The UNIVERSITY OF READING LIBRARY for their help during preparation of this article. I would also like to acknowledge COLE (1944) and FORD (1992) as the sources for much of the background material concerning the authors of the cited texts.

REFERENCES

Note : These references are to editions I have consulted in the Cole Library of Early Medicine and Zoology at Reading University.

AGASSIZ, L., 1842-1846. — *Nomenclator zoologicus, continens nomina systematica generum animalium tum viventium quam fossilium*. Solothurn, Jent et Gassmann.

ALDROVANDI, U., 1638. — *De Animalibus Insectis*. Bologna, Clement Ferroni.

BARBUT, J., 1781. *Les Genres des Insectes de Linné*. London, Jacques Dixwell, J. Sewell.

BERNARD, P., COUAILHAC, L., LEMAOUT, G. & LEMAOUT, E., 1842-1843. — *Le Jardin des Plantes. Description complète, historique et pittoresque du Muséum d'histoire naturelle, de la ménagerie, des serres, des galeries de minéralogie et d'anatomie de la vallée suisse*. Paris, L. Curmer.

BOYLE, R., 1744. — *The Works of the Honourable Robert Boyle*. London, A. Millar.

BRADLEY, R., 1721. — *A Philosophical Account of the Works of Nature*. London, W. Meare.

COLE, F. J., 1944. — *A history of comparative anatomy from Aristotle to the eighteenth century*. London, Macmillan & Co.

CUVIER, G., 1838-1849. — *Le Règne Animal distribué d'après son Organisation*. Paris, Victor Masson, 3rd "Disciples" edition.

DONOVAN, E., 1792-1807. — *The Natural History of British Insects*. London, F. & C. Rivington.

EMMET, A. M., 1991. — *The Scientific Names of the British Lepidoptera*. Colchester, Harley Books.

FORD, B. J., 1992. — *Images of Science: A History of Scientific Illustration*. London, The British Library.

GEOFFROY, E. L., 1799. — *Histoire abrégée des Insectes*. Paris, Calixte-Volland, Rémont.

GESNER, C., 1551, 1558, 1587, 1617. — *Historiae Animalium* Lib. I-V. Zurich & Frankfort, Apud Christ. Froschoverum.

GUNTHER, R. T., 1934. — *The Greek Herbal of Dioscorides*. Oxford, Oxford University Press.

HILL, J., 1752. — *A General Natural History*. Vol. III *Animals*. London, Thomas Osborne.

HOOKE, R., 1665. — *Micrographia*. London, J. Martyn & J. Allestry.

HOLLAND, P., 1601. — *The Historie of the World, commonly called The Natural Historie of C. Plinius Secundus*. Translated into English by Philemon HOLLAND, Doctor in Physicke. London, Adam Islip.

HOPKIN, S. P. & READ, H. J., 1992. — *Biology of Millipedes*. Oxford, Oxford University Press, 233 pp.

JAMES, R., 1743-1745. — *A Medical Dictionary*. London, T. Osborne.

JONSTONUS, J., 1657a. — *Historiae Naturalis. De Insectis Libri III*. Amsterdam, Apud Joannem Jacobi Fil. Schipper.

JONSTONUS, J., 1657b. — *A History of the Wonderful Things of Nature*. London, John Streater.

KIRCHER, A., 1678. — *Mundus Subterraneus*. Amsterdam, Jansson á Waesberge & Son.

KOCH, C. L., 1863. — *Die Myriapoden. Getreu nach der Natur abgebildet und beschrieben*. Halle, H.W. Schmidt.

LEEUWENHOEK, A. V., 1684-1718. — *Werken*. Leiden & Delft, Cornelius Boutesteyn, XXX pp.

LEEUWENHOEK, A. V., 1964. — *The Collected Letters of Antoni van Leeuwenhoek. Vol. 7*. Amsterdam, Swets & Zeitlinger Ltd.

Source : MNHN, Paris

LINNAEUS, C., 1735. — *Systema Naturae*. [Facsimile of the First Edition. With an Introduction and a first English translation of the "Observationes". By M. S. J. Engel-Ledeboer and H. Engel. Vol. 8 Dutch Classics on the History of Science. Nieuwkoop, B. de Graaf, 1964].

LINNAEUS, C., 1758. — *Systema Naturae. Regnum Animale. Editio decima* 1758. Cura Societatis Zoologicae Germanicae. Engelmann facsimile reprint of 1894. Tomus I, *Animals*. Leipzig, Wilhelm Engelmann.

LISTER, M., 1699. — *A Journey to Paris in the year 1698*. London, Jacob Tonson,The Second Edition.

MATTHIOLUS, P. A., 1569. — *Commentarii in sex libros Pedacii Dioscorides Anazarbei de Medica materia*. Venice, Valgrisi.

MOUFET, T., 1634. — *Insectorum sive Minimorum Animalium Theatrum*. London, Thom. Cotes.

NEWPORT, G., 1843. — On the structure, relations, and development of the nervous and circulatory systems, and on the existence of a complete circulation of the blood in vessels, in Myriapoda and Macrourous Arachnida - First Series. *Philosophical Transactions of the Royal Society* : 243-302.

OKEN, L., 1833-1842. — *Allgemeine Naturgeschichte für alle Stände*. Stuttgart, Hoffmann.

PARÉ, A., 1634. — *The Workes of that famous Chirurgion Ambrose Parey*. Translated out of Latine and compared with the French by TH. JOHNSON. London, Th. Cotes & R. Young.

PARKER, J. & HARLEY, B., 1992. — *Martin Lister"s English Spiders 1678*. Translated from the original Latin by M. DAVIES & B. HARLEY. Colchester, Harley Books.

PISO, G., 1658. — *De Indiae Utriusque Re Naturali et Medica Libri Quatuordecim Quorum contenta pagina sequens exhibet*. Amsterdam, Ludovic & Daniel Elzevir.

RONDELETIUS, G., 1554. — *Libri de Piscibus Marinis, in quibus verae Piscium effigies expressae sunt*. Lyon, Apud Matthiam Bonhomme.

SCHAEFFER, J. C., 1766. — *Elementa Entomologica*. Regensburg, Gedruckt mit Weissischen Schriften.

SEBA, A., 1735. — *Locupletissimi Rerum Naturalium Thesauri. Vol. II*. Amsterdam, Janss-Waesberge, J. Wetstein & Gul. Smith.

SHAW, G., 1800-1826. — *General Zoology or Systematic Natural History*. London, G. Kearsley.

SIBBALD, R., 1684. — *Scotia Illustrata*. Edinburgh, Jacob Kniblo, Joshua Solingen, John Colmar.

SMELLIE, W., 1790-1799. — *The Philosophy of Natural History*. Edinburgh, Charles Elliot.

STEPHENS, J. F., 1829. — *A Systematic Catalogue of British Insects*. London, Baldwin & Cradock.

SWAMMERDAM, J., 1669. — *Historia Insectorum generalis, ofte Algemeene Verhandeling van de Bloedeloose Dierkens*. Utrecht, Meinard van Dreunen.

SWAMMERDAM, J., 1758. — *The Book of Nature; or the History of Insects*. London, C.G. Seyffert.

SWAN, J., 1864. — *Illustrations of the comparative anatomy of the nervous system*. 2nd Edn. London, Bradbury & Evans.

THOMPSON, D. W. T., 1910. — *The Works of Aristotle*. Translated into English under the editorship of J. A. SMITH & W. D. ROSS. Vol. IV. Oxford, *Historia Animalium*. Clarendon Press.

TOPSEL, E., 1658. — *The History of Four-Footed Beasts and Serpents*. London, G. Sawbridge.

VON STEIN, F., 1841. — *De Myriapodum partibus genitalibus, nova generationis theoria atque introductione systematica adjectis*. Berlin, Brandes & Klewert.

WAGNER, R., 1841. — *Icones Zootomicae*. Leipzig, L. Voss.

WOTTON, E., 1552. — *De differentiis Animalium Libri Decem*. Paris, Apud Vascosanum.

Source : MNHN, Paris

An Approach to the Revision of the East Asian Millipede Genus *Anaulaciulus*

Zoltán KORSÓS

Department of Zoology, Hungarian Natural History Museum, Baross u. 13, H-1088 Budapest, Hungary

ABSTRACT

The millipede genus *Anaulaciulus* Pocock, 1895 (Julida: Julidae) comprises 44 species, distributed in Eastern Asia. Based on fresh studies of numerous samples, type material and literature, a comprehensive overview of the genus is proposed. A list of the presently known species is given, and a preliminary grouping is outlined on the basis of their posterior gonopod structure. Other external and internal characters, such as penis, gonopod promerit and female vulva structure, coloration, size, and shape of the preanal projection are discussed and evaluated. Two examples of evolutionary gonopod transformation series are presented and illustrated.

RÉSUMÉ

Essai de révision du genre est-asiatique *Anaulaciulus*.

Le genre *Anaulaciulus* Pocock, 1895 (Diplopoda, Julida, Julidae) comprend 44 espèces réparties dans l'Est asiatique. La présente révision, basée sur l'examen récent de nombreux exemplaires, permet de présenter une liste dans laquelle les espèces sont séparées en groupes provisoirement basés sur la structure des gonopodes postérieurs. D'autres caractères, externes et internes, tels que le pénis, le promérite des gonopodes, la structure des vulves, la coloration, la taille, et la forme du telson sont discutés et évalués. Deux exemples de transformation évolutive des gonopodes sont présentés et illustrés.

INTRODUCTION

The genus *Anaulaciulus* at present consists of 44 nominal species (with 4 proposed subspecies) including 10 forms recently described from the Southern Himalaya region (KORSÓS, in press). Part of the original descriptions of the other species are rather old and not properly detailed, type material of those is usually difficult to obtain. As the range of the genus (see below) implies, there may certainly be a large number of yet undiscovered species. However, considering the available material, a preliminary review of the genus seems not to be premature.

The distribution of the species in the genus includes the temperate zone of Eastern Asia: from Pakistan to the Russian Far East, through Nepal, northern India, Sikkim, Tibet, northeastern China and Korea, including Hong-Kong and Taiwan. Numerous forms occur also in Japan, south of Hokkaido (Honshu, Shikoku, Kyushu, Ryukyu Islands, Bonin Islands). To the contrast of the other widespread Eastern Asian julid genus *Nepalmatoiulus*, *Anaulaciulus*

KORSÓS, Z., 1996. — An approach to the revision of the East Asian millipede genus *Anaulaciulus*. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 35-43, Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

does not seem to penetrate into the tropical regions, it is confined to the temperate zone or high altitudes.

The genus name itself was introduced by POCOCK in 1895, and subsequently generally overlooked. The majority of the species belonging now to *Anaulaciulus* were originally described in *Fusiulus* Attems, 1909, and only in 1966 did CAUSEY recognize the synonymy with a redescription of the two POCOCK's species (*paludicola* and *vallicola*).

Anaulaciulus belongs in the tribe Brachyiulini, which can be characterized as follows:

Julidae (Brachyiulinae) without a free mesomerit on the posterior gonopod, with a well-developed flagellum, and generally compressed gonopods in the antero-posterior direction. About 24 genera are enlisted in this tribe, however, their relationship has not yet been completely clarified.

The genus *Anaulaciulus* can be defined on the basis of some peculiarities externally as well as in the gonopod conformation. The animals have no metazonal setae, no cheek lobes expanded in the males. Male gonopod promerites are characteristically flattened, scale-like, a rudiment of the telopodit is well visible. Posterior gonopods are rather simple, elongated, *in situ* always protruding from beneath protecting promerites, and have several longitudinal, slightly arched lamellae. The penis is long, bifurcate in every species; this character seems to be a unique apomorphy for the genus in the entire millipede order Julida; even the closest relatives of the genus in the tribe Brachyiulini have a completely different penis (Figs 1-3). The long, leaf-like structure (differently developed in the different species) seems to be homologuous with the apical membrane in the other species, and the opening of the seminal groove is situated most probably caudally at the basis of the "leaves".

The female vulval characters show also some peculiarities as compared to other members of the tribe. They are slightly compressed in the antero-posterior direction (others are more-or-less cylindrical), the well-separated operculum is always longer than bursa and apically provided with two lateral cusps (often also a median one). The median cleft on bursa is deep, the apodematic tube without secondary branches, the ampulla usually without an appendix.

A more detailed characterization of the genus is given elsewhere (KORSÓS, in press).

There are very few works devoted to a summary or clarification of the internal relationships of *Anaulaciulus*. An identification key is given to the species known at that time by VERHOEFF, first in 1937 (for five species), then in 1941 (for 9 species, VERHOEFF, 1941a), and by TAKAKUWA (1941, for 16 forms). They are all based mainly on minor gonopodal character details, and not very useful, especially if one regards the different quality of the descriptions and the possible morphological variations in the populations. ENGHOFF (1986) lists 28 nominal species and 6 subspecies with comments on their distribution. He establishes the synonymies of *A. ciliatus* Shinohara, 1960 and *F. trilobus quemoyensis* Wang, 1963. Apart from these, no attempt for the revision of the entire genus has been made.

REVIEW OF THE SPECIES

In the followings, a renewed alphabetical list of the presently known species in the genus is given, together with a name history and distributional data of every species. Illustrations wherever available are also referred to.

1. **Anaulaciulus acaudatus** Korsós, in press
Anaulaciulus acaudatus: KORSÓS, in press (FIGS 26-28) — India: Sikkim.

2. **Anaulaciulus acutus** (Takakuwa, 1941)
Fusiulus acutus: TAKAKUWA, 1941 (FIGS 2-3)
Anaulaciulus acutus: ENGHOFF, 1986 — Japan: Honshu.

3. **Anaulaciulus attemsii** (Verhoeff, 1941)
Fusiulus attemsii: VERHOEFF, 1941a (FIGS 31-33)
Anaulaciulus attemsii: ENGHOFF, 1986 — Japan: Honshu.

Source : MNHN, Paris

4. **Anaulaciulus bilineatus** Korsós, in press *Anaulaciulus bilineatus*: KORSÓS, in press (FIGS 2-4, 6, 9, 11, 29-33)	Nepal.
5. **Anaulaciulus bilobus** (Takakuwa, 1941) *Fusiulus bilobus*: TAKAKUWA, 1941 (FIGS 10-11) *Anaulaciulus bilobus*: ENGHOFF, 1986	Japan: Kyushu.
6. **Anaulaciulus capillatus** (Takakuwa, 1941) *Fusiulus capillatus*: TAKAKUWA, 1941 (FIGS 12-13) *Anaulaciulus capillatus*: ENGHOFF, 1986	Japan: Honshu.
7. **Anaulaciulus cornutus** (Takakuwa, 1941) *Fusiulus cornutus*: TAKAKUWA, 1941 (FIGS 17-18) *Anaulaciulus cornutus*: ENGHOFF, 1986	Japan: Kyushu.
8. **Anaulaciulus enghoffi** Korsós, in press *Anaulaciulus enghoffi*: KORSÓS, in press (FIGS 34-41)	China: Kansu.
9. **Anaulaciulus golovatchi** Mikhajlova, 1982 *Anaulaciulus golovatchi*: MIKHAJLOVA, 1982 (FIG. 2) *Anaulaciulus golovatchi*: ENGHOFF, 1986	Russia: Far East, Maritime Province; recently reported from North Korea as well (MIKHAJLOVA, 1993).
10. **Anaulaciulus hirosaminus** (Attems, 1909) *Fusiulus hirosaminus*: ATTEMS, 1909 (FIGS 76-78) *Anaulaciulus hirosaminus*: ENGHOFF, 1986	Japan: Hiro Sami.
11. **Anaulaciulus inaequipes** Enghoff, 1986 *Anaulaciulus inaequipes*: ENGHOFF, 1986 (FIGS 1-4) *Anaulaciulus inaequipes*: KORSÓS, in press (FIGS 20-25)	Burma.
12. **Anaulaciulus kashmirensis** Korsós, in press *Anaulaciulus kashmirensis*: KORSÓS, in press (FIGS 42-47)	India: Kashmir.
13. **Anaulaciulus kiusiensis** (Verhoeff, 1941) *Fusiulus kiusiensis*: VERHOEFF, 1941a (FIGS 34-36) *Anaulaciulus kiusiensis*: ENGHOFF, 1986	Japan: Kyushu.
14. **Anaulaciulus komatsui** (Shinohara, 1957) *Fusiulus komatsui*: SHINOHARA, 1957 in TAKAKUWA & SHINOHARA, 1957 (FIG. 2) *Anaulaciulus komatsui* (Takakuwa & Shinohara, 1957): ENGHOFF, 1986	Japan: Honshu.
15. **Anaulaciulus koreacolus** Jedryczkowski, 1982 *Anaulaciulus koreacolus*: JEDRYCZKOWSKI, 1982 (FIGS 28-36) *Anaulaciulus koreacolus*: ENGHOFF, 1986	Korea: Sunchon and Hyangsan districts.
16. **Anaulaciulus koreanus** (Verhoeff, 1937) *Fusiulus koreanus*: VERHOEFF, 1937 (FIGS 4-8) *Fusiulus koreanus koreanus* Verhoeff, 1937: PAIK, 1976 *Anaulaciulus koreanus*: ENGHOFF, 1986 *Anaulaciulus koreanus koreanus*: LIM, 1988	Korea: Hoko.
16.1. **Anaulaciulus koreanus boninensis** (Verhoeff, 1939) *Fusiulus koreanus boninensis*: VERHOEFF, 1939a (FIGS 16-17) *Anaulaciulus koreanus boninensis*: GOLOVATCH, 1980 (FIGS 1-2) *Anaulaciulus koreanus boninensis*: ENGHOFF, 1986	Japan: Bonin Islands, Ryukyu Islands; Korea (TAKAKUWA, 1941; PAIK, 1976; LIM, 1988; GOLOVATCH, 1980).
16.2. **Anaulaciulus koreanus tuberculatus** (Takakuwa, 1941) *Fusiulus koreanus tuberculatus*: TAKAKUWA, 1941 (FIG. 19) *Anaulaciulus koreanus tuberculatus*: ENGHOFF, 1986	Korea: Hoko (PAIK, 1976; LIM, 1988).
17. **Anaulaciulus kuritai** (Murakami, 1966) *Fusiulus kuritai*: MURAKAMI, 1966 (FIG. 1) *Anaulaciulus kuritai*: ENGHOFF, 1986	Japan: Shikoku.
18. **Anaulaciulus longus** (Takakuwa, 1941) *Fusiulus longus*: TAKAKUWA, 1941 (FIGS 6-7) *Anaulaciulus longus*: ENGHOFF, 1986	Japan: Akiyoshi; Korea (LIM, 1988).
19. **Anaulaciulus nepalensis** Korsós, in press *Anaulaciulus nepalensis*: KORSÓS, in press (FIGS 1, 3, 7, 10, 48-52)	Nepal.

Source : MNHN, Paris

20. **Anaulaciulus niger** Korsós, in press
Anaulaciulus niger: KORSÓS, in press (FIGS 53-58)
Nepal.

21. **Anaulaciulus okinawaensis** Shinohara, 1990
Anaulaciulus okinawaensis: SHINOHARA, 1990 (FIG. 1)
Japan: Ryukyu Islands.

22. **Anaulaciulus onychophora** (Takakuwa, 1942)
Fusiulus onychophora: TAKAKUWA, 1942 (FIGS 1-2)
Anaulaciulus onychophora: ENGHOFF, 1986
Japan: Honshu.

23. **Anaulaciulus otigonopus** Zhang, 1993
Anaulaciulus otigonopus: ZHANG, 1993 (FIGS 1-7)
Anaulaciulus otigonopus: KORSÓS, 1994
Anaulaciulus otigonopus: KORSÓS, in press
China: Hunan Province, Changsa.

24. **Anaulaciulus pakistanus** Korsós, in press
Anaulaciulus pakistanus: KORSÓS, in press (FIGS 59-60)
Pakistan: Swat.

25. **Anaulaciulus paludicola** Pocock, 1895
Anaulaciulus paludicola: POCOCK, 1895
Anaulaciulus paludicola: CAUSEY, 1966 (FIGS 1-6)
China: Wo-Lee Lake.

26. **Anaulaciulus pinetorum** (Attems, 1909)
Fusiulus pinetorum: ATTEMS, 1909 (FIGS 14-16, 69-75)
Fusiulus pinetorum: SHINOHARA, 1960 (FIG. 18)
Anaulaciulus pinetorum: ENGHOFF, 1986
Japan: Honshu.

26.1 **Anaulaciulus pinetorum nivalis** (Verhoeff, 1941)
Fusiulus pinetorum nivalis: VERHOEFF, 1941b (FIGS 8-10)
Fusiulus ciliatus: Shinohara, 1960 (FIGS 14-17): ENGHOFF, 1986
Anaulaciulus pinetorum nivalis: ENGHOFF, 1986
Japan: Honshu.

27. **Anaulaciulus quadratus** (Takakuwa, 1941)
Fusiulus quadratus: TAKAKUWA, 1941 (FIGS 14-16)
Anaulaciulus quadratus: TAKANO, 1978
Anaulaciulus quadratus: ENGHOFF, 1986
Japan: Honshu.

28. **Anaulaciulus riedeli** Jedryczkowski, 1982
Anaulaciulus riedeli: JEDRYCZKOWSKI, 1982 (FIGS 19-27)
Anaulaciulus riedeli: ENGHOFF, 1986
Korea: Hyangsan, Kyongsong and Puryong districts.

29. **Anaulaciulus ryugadensis** Shinohara, 1990
Anaulaciulus ryugadensis: SHINOHARA, 1990 (FIG. 2)
Japan: Shikoku.

30. **Anaulaciulus simodanus** (Takakuwa, 1941)
Fusiulus simodanus: TAKAKUWA, 1941 (FIGS 8-9)
Anaulaciulus simodanus: ENGHOFF, 1986
Japan: Honshu.

31. **Anaulaciulus simplex** Verhoeff, 1936
Fusiulus simplex: VERHOEFF, 1936
Anaulaciulus simplex: SHINOHARA, 1973
Anaulaciulus simplex: ENGHOFF, 1986
Japan: Honshu, in caves widely distributed (SHINOHARA, 1973); Taiwan (WANG, 1963; SHINOHARA, 1973).

32. **Anaulaciulus takakuwai** (Verhoeff, 1941)
Fusiulus takakuwai: VERHOEFF, 1941a (FIGS 37-38)
Anaulaciulus takakuwai: ENGHOFF, 1986
Japan: Honshu.
subspecies:
Anaulaciulus takakuwai coloratus (Verhoeff, 1941)
Fusiulus takakuwai coloratus: VERHOEFF, 1941a (FIG. 39)
Anaulaciulus takakuwai coloratus: ENGHOFF 1986
Japan: Honshu, Niijima Island.

33. **Anaulaciulus takanoi** Shinohara, 1990
Anaulaciulus takanoi: SHINOHARA, 1990 (FIG. 3)
Japan: Honshu.

34. **Anaulaciulus tibetanus** Korsós, in press
Anaulaciulus tibetanus: KORSÓS, in press (FIGS 61-63)
China: Tibet; India: Assam.

35. **Anaulaciulus tigris** Korsós, in press
Anaulaciulus tigris: KORSÓS, in press (FIGS 5, 12, 64-69)
Pakistan: Swat.

36. **Anaulaciulus tonggosanensis** Paik, 1976
Fusiulus longus Takakuwa, 1941: sensu PAIK, 1963
Fusiulus tonggosanensis: PAIK, 1976 (FIGS 1-11)
Korea: Mt. Tonggo-san (LIM, 1988).

Source : MNHN, Paris

37. **Anaulaciulus tonginus** (Karsch, 1881) *Iulus tonginus*: KARSCH, 1881 *Anaulaciulus tonginus*: ENGHOFF, 1986 *Anaulaciulus tonginus*: KORSÓS, 1994 (FIGS 1-8) *Fusiulus trilobus khuuae* Wang, 1963: KORSÓS, 1994	Hong Kong; Taiwan.
38. **Anaulaciulus topali** Korsós, in press *Anaulaciulus topali*: KORSÓS, in press (FIGS 70-75)	India: Jammu and Kashmir.
39. **Anaulaciulus trapezoidus** (Wang, 1955) *Fusiulus trapezoidus*: WANG, 1955 (FIG. 3) *Anaulaciulus trapezoidus*: ENGHOFF, 1986	Taiwan.
40. **Anaulaciulus trigonalis** (Takakuwa, 1941) *Fusiulus trigonalis*: TAKAKUWA, 1941 (FIGS 4-5) *Anaulaciulus trigonalis*: ENGHOFF, 1986	Japan: Kyushu, Kagoshima.
41. **Anaulaciulus trilobus** (Wang, 1963) *Fusiulus trilobus quemoyensis*: WANG, 1963 *Anaulaciulus trilobus*: ENGHOFF, 1986	Taiwan: Quemoy Island.
42. **Anaulaciulus vallicola** (Pocock, 1895) *Iulus vallicola*: POCOCK, 1895 (FIG. 13) *Anaulaciulus vallicola*: CAUSEY, 1966 (FIG. 7)	China: Che Kiang, Da-Zeh valley.
43. **Anaulaciulus yamashinai** (Verhoeff, 1939) *Fusiulus yamashinai*: VERHOEFF, 1939b (FIGS 1-3) *Fusiulus jamashinai* Verhoeff, 1941a (FIGS 40-42): ENGHOFF, 1986 *Fusiulus insularumi* Verhoeff, 1941a: ENGHOFF, 1986 *Fusiulus yamashinai*: TAKAKUWA, 1941 (FIG. 1) *Anaulaciulus yamashinai*: ENGHOFF, 1986	Japan: Ryukyu Islands.
44. **Anaulaciulus yosidanus** (Takakuwa, 1941) *Fusiulus yosidanus*: TAKAKUWA, 1941 (FIGS 20-21) *Anaulaciulus yosidanus*: ENGHOFF, 1986	Japan: Honshu.

INTRAGENERIC RELATIONSHIPS

The only internal classification of the genus appears in the division by VERHOEFF (1941b) where he, on the occasion of a new subspecies, *Fusiulus pinetorum nivalis*, erected the subgenus *Parfusiulus* for all the other members of the genus. The only species, *pinetorum* (with the subspecies *nivalis*) remained in the subgenus *Fusiulus* s. str. in his sense. However, the distuingishing character (i.e. two hairy fields on the mesal and lateral lamellae of the opisthomerites) seems not to be warranted, especially in the light of a more careful study of the gonopodal details in other species. As a result, virtually all species of the genus have more-or-less hairs on their opisthomerit lamellae.

According to an examination of the shape of the telopodites of the posterior gonopods, the following preliminary species-groups in the genus can be presented.

1. *yamashinai*-group (cf. Figs 8-11): *acutus, bilobus, cornutus, komatsui, onychophora, pinetorum, quadratus, trigonalis* and *yamashinai*
2. *paludicola*-group (cf. Figs 5-6): *koreacolus, longus, paludicola, riedeli, simodanus* and *tonggosanensis*
3. *koreanus*-group: *koreanus, okinawaensis, trapezoidus*
4. *hirosaminus*-group: *hirosaminus, kuritai*
5. *simplex*-group (cf. Fig. 7): *attemsii, simplex*
6. *tonginus*-group: *otigonopus, tonginus, trilobus*
7. *inaequipes*-group: *acaudatus, bilineatus, enghoffi, inaequipes, kashmirensis, nepalensis, niger, pakistanus, tibetanus, tigris* and *topali*

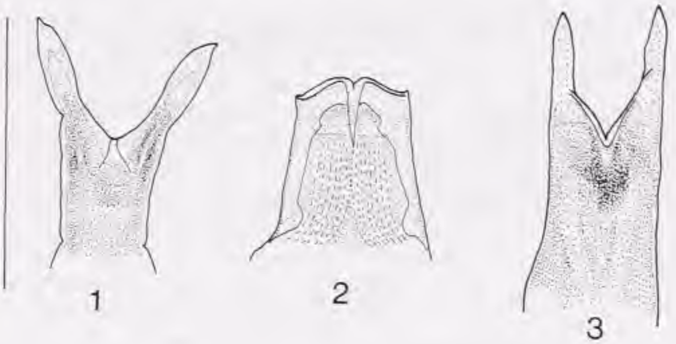
The species *takakuwai* can be considered as a bridge-species between the *paludicola*-group and the *koreanus*-group (based purely on gonopod comparison).

Source : MNHN, Paris

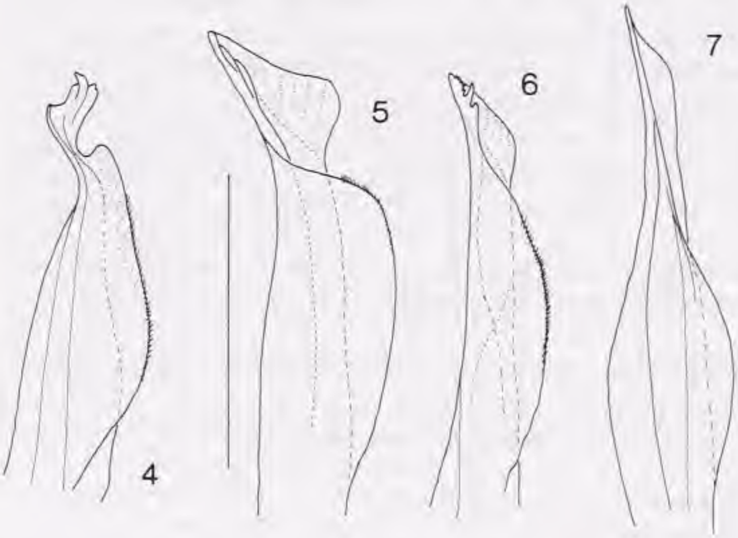
Six species could not be inserted in the groups above: *capillatus, golovatchi* (Fig. 4), *kiusiensis, ryugadensis, takanoi, yosidanus*. In some cases their gonopods are so peculiar (e.g., in *takanoi*) that even their validity within the genus *Anaulaciulus* may be question-marked. (The original description of this species does not deal with some important features like penis structure, etc.).

One species, *vallicola* is known only by female, and although the type specimen has been redescribed by CAUSEY (1966) and also seen by the author, nothing can be said about its position in the genus.

Based on some fresh material, kindly loaned by Dr. H. ONO (National Science Museum, Tokyo) some preliminary sketches are given to illustrate two main general pattern series. Figures 5 to 7 (samples from Korea and Japan) show the line of complete reduction of the opisthomerites, from a "*paludicola*"-type gonopod to a simple "needle". *Anaulaciulus golovatchi* (Fig. 4, drawn from a paratype kindly loaned by Dr. S. I. GOLOVATCH, Moscow) may perhaps also be inserted in this series.



FIGS 1-3. — Penis, caudal view. - 1: *Anaulaciulus bilineatus* Korsós, in press from Nepal. - 2: *Megaphyllum unilineatum* (C. L. Koch, 1838) from Beograd, Yugoslavia. - 3: *Anaulaciulus koreanus* (Verhoeff, 1939) from North Korea. Scale 0.5 mm.



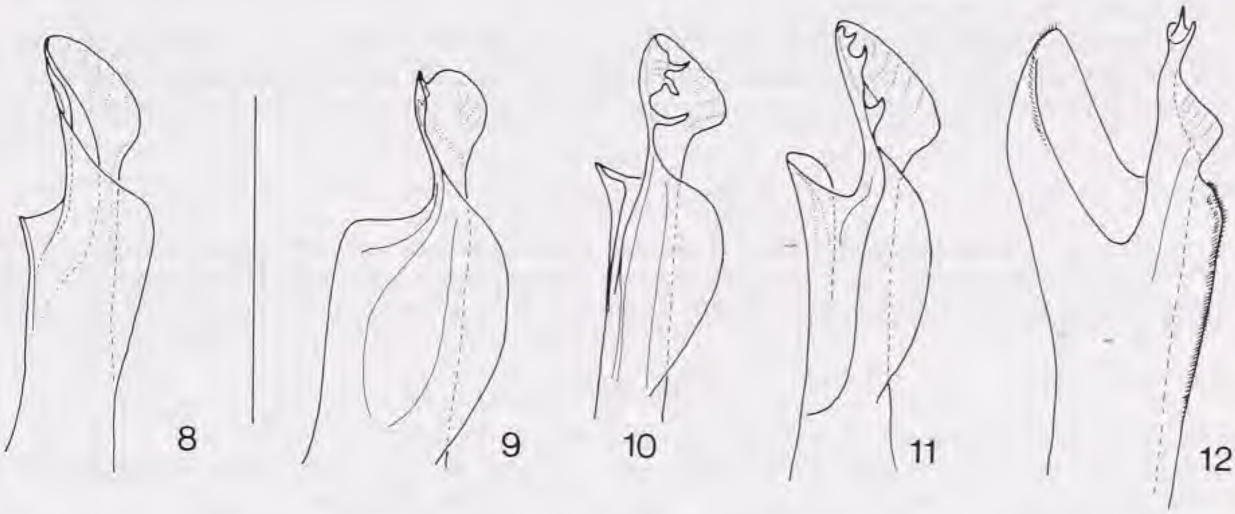
FIGS 4-7. — Left opisthomerit, frontal view. - 4: *Anaulaciulus golovatchi* Mikhajlova, 1982, paratype. - 5: Specimen from North Korea, Mt. Paekdu-san. - 6: Specimen from Japan, Ryukyu Islands, Tokara. - 7: Specimen from Japan, Ryukyu Islands, Amami. Scale 0.5 mm.

The other line is more complicated but some characteristics can be observed. The lateral lamellae of the opisthomerit appears as a "shoulder" (Fig. 8) and later, through a series of intermediates (Figs 9-11), develops into a broad "wing" (Fig. 12) as it is seen in the *inaequipes*-group. Although all this drawings are based on species originated from Japan, there is a striking resemblance between the gonopods of the specimen from Honshu (Gifu) and those of the

Source : MNHN, Paris

members of the *inaequipes*-group (cf. KORSÓS, in press). However, the lack of a proper "beak" surely allocates it in another relationship. The samples investigated for this study are certainly including several new forms, which will be dealt in future investigations.

It was already pointed out elsewhere (KORSÓS, 1994), that *Anaulaciulus tonginus* (and the similar - maybe synonymous - species, *otigonopus* and *trilobus*) is believed to have a somewhat peculiar position in the genus. Not only its intermediate penis and gonopod structure (thick, antero-posteriorly not so flattened promerites; peculiar telopodits with a beginning of a "beak" yet densely haired), but also its central geographical distribution (Hong-Kong, Taiwan, and maybe other parts of southeastern China) implies that it is close to the theoretical ancestor of the whole genus.



FIGS 8-12. — Left opisthomerite, frontal view. - 8: Specimen from Japan, Honshu, Chojaga mori. - 9: Specimen from Japan, Kyushu, Nagasaki. - 10: Specimen from Japan, Kyushu, Yaku-shima. - 11: Specimen from Japan, Kyushu, Kumamotol. - 12: Specimen from Japan, Honshu, Gifu. Scale 0.5 mm.

CONCLUSIONS

It is clear from the present observations, that the shape of the scale-like promerit is very variable in the populations and that it is not a reliable character for distinguishing species. This was already introduced by MIKHAJLOVA (1982), and further discussed by KORSÓS (in press). Unfortunately, descriptions of former species, in some cases, have been exclusively based on the shape of the promerit (e.g., *acutus*, *bilobus* & *quadratus*, all by TAKAKUWA, 1941). The degree of the morphological variability of the opisthomerites is still to be defined, and a clarification may well be resulted in a number of synonymies in the species-groups outlined above.

Female (vulval) characters, as often neglected before, are also in urgent need to redescribe. The species in the *inaequipes*-group (KORSÓS, in press) show relatively consistent pattern in the internal structure of bursa, usually having a simple or slightly curved apodematic tube and a more-or-less sphaerical ampulla; whereas other species may have more complicated apodematic tube (*golovatchi*), or an ampulla strongly elongated (*tonginus, riedeli, kiusiensis*) or with a distinct appendix (*koreanus*).

As it was shown by the analysis of the *inaequipes*-group, external characters have usually an emphasized importance in distinguishing the different species. General body colouration

Source : MNHN, Paris

(longitudinal stripes e.g., in *bilineatus*, bright yellow ground colour with dark brown blotches ordered according to pro- and metazona: as in *tigris* and *pakistanus*) is more characteristic to several species than the gonopod conformation, and may also be more useful in separating them. Outside the *inaequipes*-group, one can also find similar feature: *golovatchi*, *paludicola*, *tonginus* and *yamashinai* show three black, longitudinal stripes.

The shape of the epiproct may also help in distingushing the species, while members of the *inaequipes*-group never have a preanal project turned upwards (usually it is short, straight, or missing), the same character state, to a different degree, is not rare in the other continental and in the Japanese species (e.g., in *golovatchi*, *koreacolus*, *riedeli*, *ryugadensis*, *takanoi* & *tonginus*).

In some cases, maybe due to coexistence, significant size differences appear in closely related species-pairs (*nepalensis-niger*, *pakistanus-tigris*). This phenomenon is analyzed in more detail elsewhere (KORSÓS, in press).

Future investigations should aim at the more accurate characterization of the species, and, with the accumulation of large material from the geographically remote areas, also from Japan, the internal relationships of this highly diverse and complex genus will become possible to be clarified.

ACKNOWLEDGEMENTS

I would like to thank Dr. Henrik ENGHOFF (Copenhagen) for his kind help and continuous encouragement during my stay in the Zoologisk Museum, Copenhagen, where a part of this study was carried out. My participation at the 9th International Congress of Myriapodology in Paris and the presentation of this paper was made possible by the support of the Phare Accord Mobility Project of the National Committee for Technical Development, Hungary (Project No. 126).

REFERENCES

ATTEMS, C., 1909. — Die Myriopoden der Vega-Expedition. *Ark. Zool.*, **5** : 1-84.

CAUSEY, N. B., 1966. — Redescriptions of two Chinese species of *Anaulaciulus* (Diplopoda, Julidae, Nemasomatidae), a genus known also in Taiwan, Korea, and Japan. *Proc. Louisiana Acad. Sci.*, **29** : 63-66.

ENGHOFF, H., 1986. — Leg polymorphism in a julid millipede, *Anaulaciulus inaequipes* n. sp. With a list of congeneric species (Diplopoda, Julida, Julidae). *Steenstrupia*, **12** : 117-125.

GOLOVATCH, S. I., 1980. — A contribution to the millipede fauna of Korea (Diplopoda). *Folia ent. hung.*, **41** : 49-58.

JEDRYCZKOWSKI, W., 1982. — New and rare millipedes (Diplopoda, Julida) from North Korea. *Annls Zool. PAN*, **36** : 375-384.

KARSCH, F., 1881. — Neue Juliden des Berliner Museums, als Prodromus einer Juliden-Monographie. *Z. ges. Naturwiss.*, **54** : 1-79.

KORSÓS, Z., 1994. — Redescription of *Anaulaciulus tonginus* (Karsch, 1881) (Diplopoda, Julida, Julidae). *Steenstrupia*, **20** : 177-182.

KORSÓS, Z., (in press). — Another Himalayan group of julid millipedes: Towards the clarification of the genus *Anaulaciulus* Pocock, 1895) (Diplopoda: Julida). *Senckenbergiana biol.*

LIM, K. Y., 1988. — Taxonomical studies on Class Diplopoda from Korea. Mag. Rer. Natur. Thesis, Fac. Agric. Educ., Inst. Educ., Univ. Yuanguan., 34 pp.

MIKHAJLOVA, E. V., 1982. — New millipedes of the family Julidae (Diplopoda) from the Soviet Far East. *Zool. Zhur.*, **61** : 210-216.

MIKHAJLOVA, E. V., 1993. — The millipedes (Diplopoda) of Siberia and the Far East of Russia. *Arthropoda Selecta*, **2** : 3-36.

MURAKAMI, Y., 1966. — Postembryonic development of the common Myriapoda of Japan. XXII. Three new species of millipeds. *Zool. Mag.*, **75** : 94-97.

PAIK, K. Y., 1963. — Survey of the myriapods of Mt. Sokkri, Chungcheung-pookdo, Korea. *Theses Coll. Kyungpook Univ.*, **7** : 33-42.

PAIK, K. Y., 1976. — A new myriapod of the genus *Fusiulus* (Julidae: Diplopoda). *Theses Coll. Grad. School Educ. Kyungpook Nat. Univ.*, **6/7** : 157-160.

Source : MNHN, Paris

POCOCK, R. I., 1895. — Report upon the Chilopoda and Diplopoda obtained by P. W. Basset-Smith, Esq., Surgeon R. N., and J. J. Walker, Esq., R. N., during the cruise in the Chinese Seas of H. M. S. 'Penguin', Commander W. U. Moore commanding. *Ann. Mag. Nat. Hist., Ser. 6.*, **15** : 346-372.

SHINOHARA, K., 1960. — Three new species of Juloidea (Diplopoda) from Chichibu. *Bull. Chichibu Mus. Nat. Hist.*, **10** : 23-30.

SHINOHARA, K., 1973. — The fauna of the lava caves around Mt. Fuiji-san XIII. Diplopoda and Chilopoda. *Bull. Nat. Sci. Mus.*, **16** : 217-251.

SHINOHARA, K., 1990. — Three new species of the genus *Anaulaciulus* (Diplopoda: Julidae) from Japan. *Edaphologia*, **42** : 21-25.

TAKANO, M., 1978. — Comparative effects of BHC and Malathion against millipedes, *Anaulaciulus quadratus* (Takakuwa). *Acta Arachnol.*, **28** : 39-44.

TAKAKUWA, Y., 1941. — Die *Fusiulus*-Arten (Diplopoda). *Trans. Sapporo Nat. Hist. Soc.*, **16** : 218-226.

TAKAKUWA, Y., 1942. — Einige neue Arten von Diplopoda aus Nippon. *Zool. Mag.*, **54** : 237-239.

TAKASHIMA, H. & SHINOHARA, K., 1957. — Taxonomical and morphological study on myriapods collected in the vicinity of Towada, Tohoku District, Japan. *Misc. Rep. Yamashina Inst. Ornithol. Zool.*, **11** : 24-31.

VERHOEFF, K. W., 1936. — Über Diplopoden aus Japan, gesammelt von Herrn Y. Takakuwa. *Trans. Sapporo Nat. Hist. Soc.*, **14** : 148-172.

VERHOEFF, K. W., 1937. — Zur Kenntnis ostasiatischer Diplopoden. II. *Zool. Anz.*, **119** : 33-40.

VERHOEFF, K. W., 1939a. — Zur Kenntnis ostasiatischer Diplopoden. IV. *Zool. Anz.*, **127** : 273-285.

VERHOEFF, K. W., 1939b. — Diplopoden von der Ryukyu-Insel Okinawa. *Biogeographica. Trans. biogeogr. Soc. Japan*, **3** : 118-122.

VERHOEFF, K. W, 1941a. — Asiatische Beiträge VI. *Revue Fac. Sci. Univ. Istanbul*, **6** : 311-318.

VERHOEFF, K. W., 1941b. — Zur Kenntnis ostasiatischer Diplopoden. VI. *Zool. Anz.*, **136** : 62-70.

WANG, Y. M., 1955. — Serica 1a: Records of myriapods on Formosa with description of new species. *Quart. J. Taiwan Mus.*, **8** : 13-16.

WANG, Y. M., 1963. — Serica 1q: Millipedes and centipedes of Quemoy, Fukien Province, and Taiwan Island, Botel Tobago (Lan Yu), Taiwan Province and of Singapore. *Quart. J. Taiwan Mus.*, **16** : 89-96.

ZHANG, C., 1993. — Small myriapoda in soil from China I. A new julidan species *Anaulaciulus otigonopus* (Julida: Julidae). *Acta Zootax. Sinica*, **18** : 18-21.

Source : MNHN, Paris

Source : MNHN, Paris

The Taxa of *Rhymogona* (Diplopoda: Craspedosomatidae): a Ring Species Part One: Genetic Analysis of Population Structure

Adolf SCHOLL * & *Ariane* PEDROLI-CHRISTEN **

* Department of Population Biology, Institute of Zoology
University of Berne, Baltzerstrasse 3
CH-3012 Berne, Switzerland
** CSCF, Musée d'Histoire Naturelle, Terreaux 14
CH-2000 Neuchâtel, Switzerland

ABSTRACT

The genetic analysis of the population structure of *Rhymogona* is based on allozyme data from vertical starch gel electrophoresis (14 enzyme loci surveyed) and includes all taxa (73 collecting sites). The genetic structure of *Rhymogona* populations is not consistent with current taxonomy. We find five major groups of populations which are arranged in a circular fashion around the Jura. Adjacent groups differ from each other in allele substitutions at five polymorphic loci altogether and are connected by clinal variation. The extreme populations of this ring differ in allele substitutions at four loci. They are found in Switzerland where they obviously came into secondary contact after the last glaciation. They form narrow hybrid zones in the Jura and the Alps. Our data suggest that *Rhymogona* must be regarded as a polytypic species if the biological species concept is applied.

RÉSUMÉ

***Rhymogona* (Diplopoda, Craspedosomatidae), un genre monospécifique. Première partie : analyse génétique de la structure des populations.**

L'analyse génétique de la structure des populations de *Rhymogona* est basée sur les observations des allozymes par électrophorèse sur gel d'amidon vertical (14 loci enzymatiques) et porte sur tous les taxons de ce genre récoltés dans 73 stations. La structure génétique des populations de *Rhymogona* ne coïncide pas avec la taxinomie usuelle. Nous constatons qu'il existe cinq principaux groupes de populations, celles-ci étant distribuées de manière circulaire autour du Jura. Les groupes adjacents se distinguent par des substitutions alléliques dans cinq loci polymorphiques et sont reliés par des variations clinales. Les populations se situant aux extrêmes se distinguent par des substitutions alléliques dans quatre loci. Elles ont été recensées en Suisse où, de toute évidence, elles semblent être entrées secondairement en contact après la dernière glaciation. Elles forment d'étroites zones hybrides dans le Jura et les Alpes. Sur la base de nos résultats, *Rhymogona* doit être considéré comme espèce polytypique si l'on veut tenir compte du concept biologique de l'espèce.

SCHOLL, A. & PEDROLI-CHRISTEN, A., 1996. — The taxa of *Rhymogona* (Diplopoda: Craspedosomatidae): a ring species. Part one: genetic analysis of population structure. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 45-51. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

INTRODUCTION

Rhymogona is a small genus of the Diplopod family Craspedosomatidae which lives north of the Swiss Alps and in adjacent parts of France and Germany. Seven nominal species are recognized, most of these are known from one or a few localities only (PEDROLI-CHRISTEN & SCHOLL, this volume). We have initially attempted to study the distribution in detail (PEDROLI-CHRISTEN, 1990). Since species identification in this genus is based essentially on subtle differences in morphology of genitalia and is often not unambiguous, we have asked if enzyme electrophoretic data might be used as additional information for species identification. Our samples cover the whole area of distribution of *Rhymogona* and all taxa described (73 collecting sites).

MATERIAL AND METHODS

The collecting sites are shown in Fig. 1 and are listed in Table 1 along with the species diagnosis based on morphological criteria (PEDROLI-CHRISTEN & SCHOLL, this volume, for details of taxonomy and identification). The specimens were stored at -80°C prior to electrophoresis. Electrophoretic studies (vertical starch gel electrophoresis) were conducted using routine techniques of our laboratory (cf. SCHOLL *et al.*, 1990; PEDROLI-CHRISTEN & SCHOLL, 1990). We have scored 14 loci: Apk, Got-1, Got-2, α-Gpd, Gpt, Hk, Idh, Mdh-1, Mdh-2, Mod, Mpi, 6Pgd, Pgi and Pk. Five loci were polymorphic and indicated genetic differentiation among populations: Got-1, Mpi, 6Pgd, Pgi and Pk.

Mendelian inheritance of the electromorphs observed could not be assessed by breeding experiments but is assumed by analogy (cf. ZIMMERMANN & SCHOLL, 1993). Due to initial difficulties in resolving Mpi, this enzyme was not scored in some populations (Table 1). The designation of alleles is based on electrophoretic mobilities (in mm) of the electromorphs; *R. montivaga* from the Alps (sites 2-5 in Table1 and Fig. 1) were used as reference (assigned index = 100 for the common allele at each locus). Coefficients of genetic identity (I) were calculated in pairwise comparisons of the populations using the formula given by NEI (1972). These coefficients served as a matrix for average linkage cluster analysis (UPGMA) (NEI, 1987).

RESULTS AND DISCUSSION

Table 1 shows the allele frequencies at five polymorphic loci. We have not listed seven very rare alleles which were observed at one or the other locus in nine populations altogether. These alleles do not contribute to the outline of the *Rhymogona* population structure presented. Sample sizes were very low in some collecting sites. We have listed these sites in Table 1, but samples with < 5 specimens were not included in further treatment of data because adequate sample sizes are critical in genetic analysis of populations. Identification of individuals based on morphology suggested that several samples contained more than one taxon (e.g. sites 27, 33, 53 in Table 1 and Fig. 1). The electrophoretic data, however, gave no evidence for the coexistence of genetically separated gene pools at these sites or at any other site. With respect to the enzyme phenotypes observed, we found no significant deviations from HARDY-WEINBERG expectations. For calculations of allele frequencies and further treatment of data we have pooled all specimens of a particular site.

Two alleles were found at the Got-1 locus, Got-1^{100} and Got-1^{96} respectively. In most populations, however, one or the other allele was fixed. Allele Got-1^{100} was observed in most *R. montivaga* populations (sites 1 - 11 in Table 1), *montivaga* populations from the western part of the Swiss Jura (sites 12 - 14) were polymorphic, French *R. montivaga* populations (sites 15 - 16) instead had allele Got-1^{96} fixed as all other populations and taxa except *montivaga/cervina* hybrid populations (sites 67 - 73).

Two alleles were found at the 6-Pgd locus, 6-Pgd^{100} and 6-Pgd^{94} respectively. Allele 6-Pgd^{100} was fixed in all populations and taxa except the Swiss *R. cervina* populations. The *R. cervina* populations in the Swiss Jura (sites 55 - 62) had allele 6-Pgd^{94} fixed; *R. cervina* populations along the Rhine (sites 44 - 47, 50 and 53), populations from the *cervina/alemannica* contact zone in the Swiss Jura (sites 26, 27) and populations from the *montivaga/cervina* hybrid zone in the Swiss Jura and the Alps (sites 65 - 73) were polymorphic.

Source : MNHN, Paris

	Sampling Site	Taxon (based on morphology)	number of specimens	Got-1 96	Got-1 100	6Pgd 94	6Pgd 100	Pk 94	Pk 100	Pgi 100	Pgi 103	Mpi 100	Mpi 102	no activity
1	Leukerbad	*m. montivaga*	4		1.00		1.00		1.00	1.00		-		
2	Gemmi	*m. montivaga*	16	0.16	0.84		1.00		1.00	1.00		0.37		0.63
3	Iffigenalp	*m. montivaga*	13		1.00		1.00		1.00	0.96		0.96	0.04	
4	Sanetsch	*m. montivaga*	12		1.00	0.04	0.96		1.00	1.00		1.00		
5	Lauenen	*m. montivaga*	13		1.00		0.96		1.00	1.00		1.00		
6	Tour de Famelon	*m. montivaga*	7		1.00		1.00		1.00	1.00		1.00		
7	Morgins	*m. montivaga*	4		1.00		1.00		1.00	1.00		1.00		
8	Vouvry	*m. montivaga*	1		1.00		1.00		1.00	1.00		-		
9	Rochers de Naye	*m. montivaga*	1		1.00		1.00		1.00	1.00		-		
10	Lessy	*m. montivaga*	1		1.00		1.00		1.00	-		-		
11	Le Cachot	*m. montivaga*	1		1.00		1.00		1.00	1.00		-		
12	La Brévine	*m. montivaga*	19	0.05	0.95		1.00		1.00	1.00		1.00		
13	Mauborget	*m. montivaga*	64	0.10	0.90		1.00		1.00	1.00		0.89	0.12	
14	St. Georges	*m. montivaga*	39	0.19	0.81		1.00		1.00	1.00		1.00		
15	Grande Chartreuse	*m. montivaga*	10	1.00			1.00		1.00	1.00		1.00		
16	Levier	*m. montivaga*	11	1.00			1.00		1.00	1.00		0.96	0.04	
17	Deschaux	*m. hessei*	4	1.00			1.00		1.00	1.00		1.00		
18	Médière	*m. hessei*	8	1.00			1.00		1.00	1.00		0.90	0.10	
19	Belverne	*m. hessei*	7	1.00			1.00		1.00	1.00		0.21	0.79	
20	Beaune	*m. hessei*	1	1.00			1.00		1.00	1.00			1.00	
21	Ancey	*montivaga-group**	1	1.00			1.00		1.00	1.00			1.00	
22	Lantenay	*montivaga-group**	1	1.00			1.00		1.00	1.00			1.00	
23	Vernot	*m. hessei*	10	1.00			1.00		1.00	1.00			1.00	
24	Courtedoux	*alemannica*	46	1.00			1.00	0.81	0.19	1.00			0.96	
25	Noir Bois	*alemannica*	28	1.00			1.00	0.86	0.14	1.00			1.00	
26	Le Breuil	*cervina, alemannica***	3	1.00		0.83	0.17	0.83	0.17	1.00			1.00	
27	St. Ursanne	*cervina, alemannica***	31	1.00		0.38	0.63	0.96	0.04	0.98			1.00	
28	Bonfol	*alemannica*	1	1.00			1.00	1.00		1.00			1.00	
29	Boncourt	*alemannica ?*	4	1.00			1.00	0.50	0.50	1.00			1.00	
30	Masevaux	*alemannica*	5	1.00			1.00	1.00		1.00			1.00	
31	Le Haut-du-Them	*alemannica*	2	1.00			1.00	1.00		1.00			1.00	
32	Linthal	*alemannica*	8	1.00			1.00	1.00		1.00			1.00	
33	Kenzingen	*cervina + alemannica ?*	5	1.00			1.00	1.00		1.00			1.00	-
34	Hornberg	*cervina, verhoeffi***	3	1.00			1.00	1.00		1.00			1.00	
35	Marbach	*cervina-group**	2	1.00			1.00	1.00		1.00			1.00	
36	Badenweiler	*alemannica*	25	1.00			1.00	0.88	0.10	1.00			1.00	
37	Ottwangen	*serrata*	23	0.91	0.07		1.00	0.39	0.61	1.00			0.98	
38	Inzlingen	*serrata*	10	1.00			1.00	0.20	0.80	0.85	0.15		1.00	
39	Hasel	*wehrana*	26	1.00			1.00	1.00		0.98	0.02		1.00	
40	Todtmoos	*wehrana*	20	1.00			1.00	0.95	0.05	0.95			1.00	
41	Menzenschwand	*wehrana*	3	1.00			1.00	1.00		1.00			-	
42	Laufenburg	*verhoeffi*	5	1.00			1.00	1.00			1.00		0.37	0.63
43	Tiefenstein	*verhoeffi*	5	1.00			1.00	1.00		0.10	0.90		1.00	
44	Sulz	*cervina-group**	7	1.00		0.29	0.71	1.00		0.86	0.14		0.93	
45	Schupfart	*cervina-group**	4	1.00		0.50	0.50	1.00		1.00			0.50	0.50
46	Homburg	*cervina*	16	1.00		0.32	0.68	1.00		0.97	0.03		1.00	
47	Küssnach	*cervina*	4	1.00		0.13	0.88	1.00		1.00			0.50	
48	Altglashütten	*cervina + verhoeffi ?*	4	1.00			1.00	1.00		1.00			1.00	
49	Gutachbrücke	*verhoeffi, wehrana***	4	1.00			1.00	0.50	0.50	1.00			0.75	
50	Husmersee	*cervina*	11	1.00		0.70	0.30	1.00		1.00			1.00	
51	Dissenhofen	*cervina*	2	1.00			1.00	1.00		1.00				1.00
52	Hemishofen	*cervina*	14	1.00			1.00	1.00		1.00				1.00
53	Staad	*cervina, alemannica***	8	1.00		0.13	0.88	1.00		1.00			1.00	
54	Baar	*cervina*	36	1.00		0.95	0.05	0.99		1.00			0.02	0.98
55	Obergütsch	*cervina ?*	2	1.00		1.00		0.75	0.25	1.00			1.00	
56	Trub	*cervina*	7	1.00		0.86	0.14	1.00		1.00				1.00
57	Schelten	*cervina*	4	1.00		1.00		1.00		1.00			-	
58	Berlincourt	*cervina*	20	1.00		1.00		1.00		1.00			0.61	0.39
59	Gorges de Court	*cervina*	3	1.00		1.00		0.33	0.67	1.00			1.00	
60	Combe Biosse	*cervina*	5	1.00		1.00		1.00		1.00				1.00
61	Pertuis	*cervina*	20	1.00		1.00		1.00		1.00			1.00	
62	Prévoux	*cervina*	52	0.99	0.01	0.97	0.03	0.76	0.21	1.00			0.65	0.35
63	Valsainte	*cervina-group**	1	1.00			1.00	1.00		1.00				1.00
64	Schwarzenmatt	*cervina*	3	1.00		1.00		0.33	0.67	1.00			0.18	0.82
65	Jaun	*cervina-group**	3	1.00		0.83	0.17	1.00		1.00				1.00
66	Kandersteg	*cervina*	20	0.95	0.05	0.95	0.05	0.58	0.43	1.00		0.08		0.92
67	Zweisimmen	*cervina / montivaga*	20	0.48	0.53	0.15	0.85	0.25	0.75	1.00		0.28	0.42	0.30
68	Boltigen	*cervina / montivaga*	25	0.78	0.22	0.75	0.25	0.71	0.30	1.00		0.15		0.85
69	Peseux	*cervina / montivaga*	27	0.43	0.57	0.71	0.29	0.06	0.94	1.00		1.00		
70	Rochefort	*cervina / montivaga*	3	0.67	0.33	0.83	0.17	-		-		-		
71	Mauvaise Combe	*cervina / montivaga*	12	0.67	0.33	0.46	0.54	0.13	0.88	1.00		-		
72	La Chaux-du-Milieu	*cervina / montivaga*	39	0.67	0.33	0.60	0.40	0.18	0.82	1.00		-		
73	Verrières	*cervina / montivaga*	38	0.84	0.16	0.57	0.43	0.03	0.93	1.00		0.47	0.05	0.48

TABLE 1. — Allele frequencies at five polymorphic loci (rare alleles are not listed). * = females only; ** = identification ambiguous; sites 67-73 = *cervina/montivaga* hybrid populations.

Source : MNHN, Paris

Two alleles, Pk^{100} and Pk^{94} respectively, were found at the Pk locus. Allele Pk^{100} was fixed in all *R. montivaga* populations. Polymorphism was observed in *R. alemannica* populations from the Swiss Jura (sites 24 - 29), in populations from the southwestern Black Forest region (sites 36 - 40) which were keyed out as *alemannica*, *serrata* and *wehrana*, and in the *montivaga /cervina* hybrid zone.

FIG. 1. — Sampling sites of electrophoretically analysed *Rhymogona* specimens (species diagnosis based on morphological criteria).

At the Pgi locus most populations were monomorphic for allele Pgi^{100}. A second allele, Pgi^{103}, was observed in low frequencies or even fixed in six populations from the southern Black Forest region, including the taxa *serrata*, *wehrana*, *verhoeffi* and *cervina*, as shown in Table 1.

Due to initial difficulties in resolving Mpi, this enzyme was not scored in all populations. Furthermore, many specimens, in particular those from *R. cervina* populations in Switzerland and those from *montivaga/cervina* hybrid populations, failed to show Mpi activity. Possibly this is due to the presence of a null allele. For calculation of Mpi allele frequencies we have assumed that specimens with no Mpi activity are homozygous for a null allele.

Source : MNHN, Paris

In populations of *R. montivaga* and in *montivaga/cervina* hybrid populations we scored the allele Mpi^{100}. Populations of other taxa were usually monomorphic for Mpi^{102}, except two populations from the French Jura (sites 18 and 19), both keyed out as *R. m. hessei*, which were polymorphic. The allele frequencies observed in these two populations suggested clinal variation towards populations from the Vosges.

Cluster analysis of coefficients of genetic identity (I) (populations from the *montivaga/cervina* hybrid zone, sites 66 - 73, not included) resulted in several major groups of populations with very high levels of genetic identity (I > 0.98). These groups are shown in Fig. 2. Group A has the Swiss *R. montivaga* populations; group B has French populations keyed out as *R. m. montivaga* and *R. m. hessei* respectively; group C has *m. hessei* populations; group D has the northern *Rhymogona* populations and includes the taxa *alemannica, cervina*, and *wehrana*; groups E and F have *R. serrata* and *R. verhoeffi*, respectively; group G has the Swiss *R. cervina* populations and includes specimens from the type locality of *R. aelleni* (site 54). These groups usually differ, in the order as they are presented, by allele substitution at one locus (Fig. 2). Group E which has the two *R. serrata* populations is exceptional because it is polymorphic at the Pk locus and therefore has an intermediate position between groups C and D. According to the allele frequencies observed (Table 1) group E is more close to group C with respect to genetic identity.

FIG. 2. — Genetic differentiation of *Rhymogona* populations.

Source : MNHN, Paris

It is important, however, to realize that the differentiation among these groups is not abrupt. The allele substitutions observed between population groups change in a clinal fashion. These clines appear to be shallow in some regions and steeper in other regions, as far as we can see from a rather limited number of individuals and/or populations in some areas.

More generally, the electrophoretic data show that the genetic structure of *Rhymogona* populations is not consistent with current taxonomy. This is most clearly evident from a comparison of populations from the Black Forest region and from the Vosges (group D in Fig. 2), which include the taxa *alemannica*, *cervina* and *wehrana* according to morphology. These populations are largely identical with respect to the alleles observed and to their frequencies (Table 1). In contrast, *R. cervina* populations from Switzerland are different from *R. cervina* populations in the Black Forest region. Furthermore, *R. verhoeffi*, which has the allele Mpi^{103} substituted for Mpi^{100}, is clearly differentiated from the other taxa, however, Mpi^{103} is also observed in low frequencies in other populations from nearby localities (sites 38, 39, 44 and 46 in Table 1 and Fig. 1). These specimens were keyed out as *serrata*, *wehrana*, and *cervina* respectively. The electrophoretic data suggest gene flow among these taxa and an isolation-by-distance model of genetic differentiation.

The more relevant information obtained from the electrophoretic survey are the observations that the alleles and their frequencies change largely independently of morphological characters and that they change in a clinal fashion within and among taxa. The groups of populations are arranged in a more or less circular fashion around the Jura. Groups A and G, which have obviously colonized this area after the last glaciation, come into secondary contact in the Swiss Jura and in the Alps. These two groups differ by allele substitution in four loci, and they form rather narrow hybrid zones in the Swiss Jura and the Alps, as we have shown previously (PEDROLI-CHRISTEN & SCHOLL, 1990).

CONCLUSIONS

Rhymogona species, as in most other diplopods, were initially described using the morphospecies concept. Other species concepts have been developed since (cf. HAFFNER, 1986). The biological species concept which defines species as "groups of interbreeding natural populations that are reproductively isolated from other such groups" (MAYR, 1969) is now chosen by the majority of zoologists (MAYR, 1963, 1970; HEWITT, 1990). As summarized in Figure 2, our data show that *Rhymogona* consists of groups of genetically differentiated populations. However, there is no evidence that these groups are reproductively isolated. In contrast, our data show that there is gene flow between these groups. Our results therefore have taxonomic consequences and suggest that *Rhymogona* must be regarded as a polytypic species. All species presently recognized should be revised to subspecies of *Rhymogona montivaga* as will be discussed (PEDROLI-CHRISTEN & SCHOLL, this volume).

ACKNOWLEDGEMENTS

We are indepted to Mrs. V. SIEGFRIED and Mrs. L. FRAUCHIGER for technical assistance in the electrophoretic studies and to S. HUNZIKER for computer graphics. Critical comments and suggestions of Dr. Henrik ENGHOFF and Dr. Adam H. PORTER and Dr. John R. SPENCE on an earlier version of this manuscript are gratefully acknowledged.

REFERENCES

HAFFNER, J., 1986. — Superspecies and species limits in vertebrates. *Z. zool. Syst. Evolutionsforsch.*, **24** : 169-190.

HEWITT, G. M., 1990. — Divergence and speciation as viewed from an insect hybrid zone. *Can. J. Zool.*, **68** : 1701-1715.

MAYR, E., 1963. — *Animal species and evolution*. Cambridge, Massachusetts, Harvard University Press.

MAYR, E., 1969. — *Principles of systematic zoology*. New York, McGraw-Hill.

MAYR, E., 1970. — *Populations, species and evolution*. Cambridge, Massachusetts, Belknap Press of Harvard University.

NEI, M., 1972. — Genetic distance between populations. *Am. Nat.* **106** : 283-292.

Source : MNHN, Paris

NEI, M., 1987. — *Molecular evolutionary genetics*. New-York, 512 pp.

PEDROLI-CHRISTEN, A., 1990. — Field investigations on *Rhymogona cervina* Verhoeff and *Rhymogona silvatica* Rothenbühler (Diplopoda): Morphology, distribution and hybridization. *In* : A. MINELLI, *Proc. 7th int. Congr. Myriapodology*. Leiden, E. J. Brill : 27-43.

PEDROLI-CHRISTEN, A. & SCHOLL, A., 1990. — Ecological and genetic studies on parapatric *Rhymogona silvatica* Roth. and *R. cervina* Verh. (Diplopoda: Craspedosomatidae) with special reference to hybrid populations in a zone of contact. *Rev. suisse Zool.*, **97**, 349-359.

SCHOLL, A., OBRECHT, E. & OWEN, R. E., 1990. — The genetic relationship between *Bombus moderatus* Cresson and the *Bombus lucorum* auct. species complex (Hymenoptera: Apidae). *Can. J. Zool.*, **68** : 2264-2268.

ZIMMERMANN, M. & SCHOLL, A., 1993. — Specific status of *Aquarius cinereus* (Puton) and *Aquarius najas* (De Geer) (Hemiptera: Gerridae) and the extent of hybridisation in the Mediterranean region. *Ent. scand.*, **24** : 197-210.

Source : MNHN, Paris

Source : MNHN, Paris

Rhymogona (Diplopoda, Craspedosomatidae), un genre monospécifique. Deuxième partie : Révision basée sur les résultats morphologiques, génétiques et faunistiques

Ariane PEDROLI-CHRISTEN * & *Adolf* SCHOLL **

* C.S.C.F., Musée d'Histoire Naturelle, Terreaux 14, CH-2000 Neuchâtel, Suisse
** Département Biologie des Populations, Institut de Zoologie, Université de Berne
Baltzerstrasse 3, CH-3012 Berne, Suisse

RÉSUMÉ

La révision du genre *Rhymogona*, qui comprend selon la bibliographie sept taxons nominaux, est basée sur des observations faunistiques et morphologiques (analyse des genitalia) ainsi que sur des résultats génétiques, présentés dans la première partie de ce travail (SCHOLL & PEDROLI-CHRISTEN, ce volume). Le taxon *aelleni* (Schubart, 1960) est mis en synonymie avec *cervina*. Nous reconnaissons une espèce polytypique, *Rhymogona montivaga* (Verhoeff, 1894) ; les taxons *cervina* (Verhoeff, 1910), *alemannica* (Verhoeff, 1910), *verhoeffi* (Bigler, 1913) *serrata* (Bigler, 1913) et *wehrana* (Verhoeff, 1910) sont considérés comme des sous-espèces.

ABSTRACT

***Rhymogona* (Diplopoda, Craspedosomatidae), a ring species. Second part: revision based upon morphological, genetic and faunistic results.**

The revision of the genus *Rhymogona*, which houses seven nominal species according to previous authors, is based on faunistic and morphological studies (analysis of genitalia) and on genetic data, presented in part I of this work (SCHOLL & PEDROLI-CHRISTEN, this volume). The taxon *aelleni* (Schubart, 1960) is placed in synonymy with *cervina* (Verhoeff, 1910). We recognize a polytypic species, *Rhymogona montivaga* (Verhoeff, 1894); the taxa *cervina* (Verhoeff, 1910), *alemannica* (Verhoeff, 1910), *verhoeffi* (Bigler, 1913) *serrata* (Bigler, 1913) and *wehrana* (Verhoeff, 1910) are revised to subspecies.

INTRODUCTION

Plusieurs travaux concernant le genre *Rhymogona* ont fait l'objet de publications récentes. PEDROLI-CHRISTEN (1990) résume, selon les données bibliographiques, la répartition géographique des diverses espèces alors recensées pour le genre et l'état des connaissances systématiques. Par ailleurs, des recherches faunistiques récentes permettent de mettre en évidence des zones de contact entre deux taxons, *montivaga* (syn. *silvatica* voir PEDROLI-CHRISTEN & SCHOLL, 1991) et *cervina* dans le Jura et les Préalpes suisses. L'analyse

PEDROLI-CHRISTEN, A. & SCHOLL, A., 1996. — *Rhymogona* (Diplopoda, Craspedosomatidae), un genre monospécifique. Deuxième Partie : Révision basée sur les résultats morphologiques, génétiques et faunistiques. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 53-60. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

morphologique des genitalia des individus mâles et femelles en provenance de ces zones mène à l'hypothèse de l'existence de phénomènes d'hybridation entre ces deux taxons.

Le recours à des analyses génétiques (électrophorèses enzymatiques) complémentaires permet de confirmer cette hypothèse (PEDROLI-CHRISTEN & SCHOLL, 1990). Les résultats obtenus relativisent le statut d'espèce attribué à ces deux taxons. Afin de mieux comprendre la systématique de *Rhymogona*, un élargissement de la recherche à l'ensemble du genre sur toute son aire de répartition (Suisse, Nord des Alpes ; alentours de la Forêt Noire en Allemagne ; en France, de l'Alsace et des Vosges à la Savoie) a été effectué. Les résultats obtenus sont présentés en deux parties, fortement imbriquées : - la première partie (cf. Part 1, ce volume), fait état des analyses génétiques de structures des populations et mène à la notion de "ring species" - la deuxième partie présente les conséquences systématiques des résultats sous forme d'une révision du genre.

MATÉRIEL ET MÉTHODES

Le matériel a été récolté par chasse-à-vue sous des écorces et bois morts au sol dans 250 sites répartis sur l'ensemble de l'aire de répartition du genre, surtout en septembre et octobre, de 1986 à 1991. 925 individus collectés en 73 stations ont fait l'objet d'analyses morphologiques et génétiques (Tableau 1 et Fig. 1 *in* SCHOLL & PEDROLI-CHRISTEN, Part I).

Le matériel récent a été comparé pour identification aux figures et descriptions des auteurs, mais aussi au matériel original de VERHOEFF et de BIGLER.

Collection VERHOEFF, Staatssammlung de Munich :

R. alemannica (VERHOEFF, 1916, Staad/Rorschach; VERHOEFF, 1935, Mindelsee) ; *R. a. rotundatum* (VERHOEFF, 1916, Badenweiler) ; *R. cervina* (VERHOEFF, 1910, Pratteln, Schönberg bei Freiburg; VERHOEFF, 1916, Sulz bei Laufenburg, Immendingen) ; *R. c. brevidentatum* (VERHOEFF, 1916, Tiengen) ; *R. verhoeffi* (VERHOEFF, 1916, Rottweil am Neckar) ; *R. v. excavatum* (VERHOEFF, 1916, Andelsbachtal bei Klein-Laufenburg) ; *R. wehrana genuinum* (VERHOEFF, 1910 Wehr, VERHOEFF, 1936 Höllental) ; *R. wehrana clavigerum* (VERHOEFF, 1935, Schönau) ; *R. wehrana calcivagum* (VERHOEFF, 1910, Wehr) ; *R. wehrana quadridentatum* (VERHOEFF, 1935, Zell).

Collection BIGLER, Musée d'Histoire Naturelle de Bâle :

R. alemannica (Vogesen, Sondernach, Nenzlingen, N'Lauchen, Tschäpperli, Reinacherallmend) ; *R. a. triarticulatum* (Bellackerkopf, Linthal, Sondernach) ; *R. a. globosum* (N'Lauchen, Hochfeld) ; *R. a. alsaticum* (Glasbächli) ; *R. cervina* (Guldental, Oberdornach) ; *R. verhoeffi* (Gutach) ; *R. serrata* (Ottwangen, Hagenbach).

HISTORIQUE

- VERHOEFF (1894) décrit *Atractosoma montivagum*. Rochers de Naye (Vaud/CH) et Daubensee (Valais/CH).
- COOK (1896) crée le genre *Rhymogona* qui reste oublié jusqu'au travail de HOFFMAN (1980).
- VERHOEFF (1897) crée le genre *Macheiriophoron*, couramment utilisé par la suite.
- ROTHENBÜHLER (1899) décrit *A. montivagum silvaticum* (Villeneuve Vaud/CH).
- VERHOEFF (1910) décrit *M. alemannicum*, Hohentwil et Rufach en Alsace(F) ; *M. cervinum*, Schönberg bei Freiburg (D) et Pratteln (Basel/CH) ; *M. wehranum*, Wehr (ouest) dans le Wehratal (D). Il attribue le statut d'espèce à *M. silvaticum* décrit par ROTHENBÜHLER (1899).
- BIGLER (1913) décrit *M. verhoeffi*, Gutach en Forêt Noire et *M. serratum*, Ottwangen et Hagen au Dinkelberg (D) près de Bâle.
- SCHUBART (1960) décrit *M. aelleni*, grotte de Baar (Zoug/CH).

Des sous-espèces ou variétés ont été décrites pour pratiquement toutes les espèces :

- BROLEMANN (1935) *M. silvaticum hessei*, Prenois, Côte d'Or (F).
- BIGLER (1913) *M. alemannicum genuinum*, Jura Suisse, rive gauche de la Birse ; *M. alemannicum globosum*, Niederlauchen en Alsace (F) ; *M. alemannicum triarticulatum*, vallées dans le sud des Vosges (F).
- VERHOEFF (1916) *M. alemannicum rotundatum*, Badenweiler (D).
- VERHOEFF (1916) *M. cervinum brevidentatum*, Tiengen und Thalmühle (D).

Source : MNHN, Paris

- VERHOEFF (1910) *M. wehranum calcivagum*, Wehr (est) dans le Wehratal (D).

- VERHOEFF (1935) *M. wehranum clavigerum*, Schönau dans le Wiesetal (D) ; *M. w. quadridentatum*, Zell dans le Wiesetal (D).

- VERHOEFF (1916) *M. verhoeffi excavatum*, Andelsbachtal bei Klein-Laufenburg (D).

- PEDROLI-CHRISTEN & SCHOLL (1991) proposent de considérer *R. silvatica* comme synonyme de *R. montivaga* sur la base des analyses morphologiques et génétiques.

MORPHOLOGIE COMPARÉE DES GENITALIA FEMELLES

Pour tous les taxons sus-mentionnés deux types de structures de vulves des femelles sont reconnaissables, soit celui de *R. montivaga hessei* (RAVOUX, 1942) et *R. montivaga* (PEDROLI-CHRISTEN, 1990) chez qui la valve externe est courte et la valve interne longue, soit celui de *R. alemannica* (VERHOEFF, 1913) et *R. cervina* (PEDROLI-CHRISTEN, 1990), chez qui la valve externe est longue et la valve interne courte.

Les taxons *R. montivaga, R. wehrana* et *R. serrata* ont une morphologie vulvaire du premier type et sont difficilement discernables les uns des autres. *R. alemannica, R. cervina* et *R. verhoeffi* présentent le deuxième type morphologique et ne peuvent pas être distingués les uns des autres. Ceci est d'autant plus valable pour leurs sous-espèces respectives.

MORPHOLOGIE COMPARÉE DES GONOPODES

Taxons ***montivaga***, ***wehrana*** et ***serrata*** (Fig. 1 A, B, C)

La détermination de ces trois taxons, géographiquement bien séparés, ne présente en principe pas trop de difficultés. Cependant, relevons la variabilité existant à l'intérieur même de chaque espèce morphologique et ceci essentiellement pour la structure des cheirites et des paragonopodes (PEDROLI-CHRISTEN, 1990; PEDROLI-CHRISTEN & SCHOLL, 1991 pour *R. montivaga*).

Le fait que VERHOEFF ait décrit autant de formes appartenant au taxon *wehrana* va dans le même sens. La forme *calcivagum*, qui ne présente plus le crochet caractéristique à la base du cheirite, ressemble alors très fortement à *R. montivaga*. Rappelons ici qu'à l'inverse, plusieurs mâles en provenance des zones hybrides localisées dans le Jura Suisse présentent, contrairement aux deux formes parentales *montivaga* et *cervina*, un cheirite très semblable à celui de *R. wehrana* (Fig. 1, B et Fig. 8 *in* : PEDROLI-CHRISTEN, 1990).

Les différences morphologiques entre *montivaga* et *montivaga hessei* sont très faibles et se situent au niveau de l'extrémité de la corne rostrale qui est aplatie et accompagnée d'une lamelle chez la sous-espèce.

Taxons ***cervina***, ***aelleni***, ***alemannica*** et ***verhoeffi***

a) *cervina* (Fig. 1 E, F)

Ce taxon se distingue, selon VERHOEFF (1910 et 1916) :

- au syncolpocoxite: par une longue corne rostrale falciforme (raccourcie chez *brevidentatum*) à peine plus courte que la lame en faucille ; par une courbe de la lame en faucille simple et ne présentant pas de dent triangulaire, tout au plus une ou deux petites pointes ;

- au cheirite : par le prolongement basal du cheirite en général resserré vers le haut et vers le bas ainsi qu'une pointe dressée bien développée.

L'observation des mâles en provenance de 16 populations (cf. Table 1, Part 1) amène à nuancer certains de ces points :

- la longueur de la corne rostrale est variable selon les populations et, souvent, à l'intérieur même d'une population (la distance entre la pointe de la lame en faucille et la pointe de la corne rostrale varie entre 0 (les deux pointes se juxtaposent) et 0,13mm (ce que l'on observe pour *R. alemannica*) ;

Source : MNHN, Paris

- si certaines populations présentent une lame en faucille à courbe simple (ex. stations 33, 48, 46 ou 50, Part 1) beaucoup d'autres développent une dent bien marquée (Fig. 1 E, G ; Fig. 6B *in* : PEDROLI-CHRISTEN, 1990). Les deux variantes ont été observées, par exemple, dans des populations du Jura (stations 61, 62) ou à Baar (54).

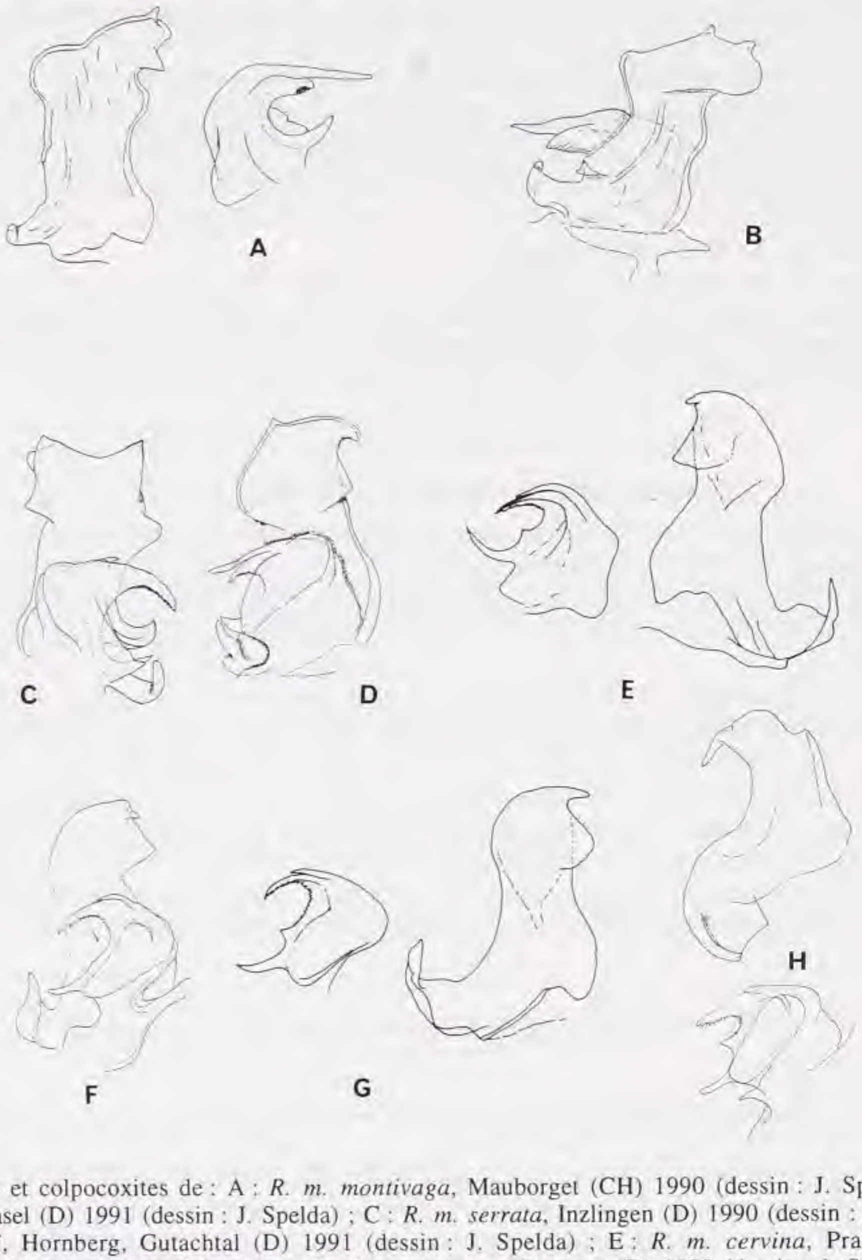


FIG. 1. — Cheirites et colpocoxites de : A : *R. m. montivaga*, Mauborget (CH) 1990 (dessin : J. Spelda) ; B : *R. m. wehrana*, Hasel (D) 1991 (dessin : J. Spelda) ; C : *R. m. serrata*, Inzlingen (D) 1990 (dessin : J. Spelda); D : *R. m. verhoeffi*, Hornberg, Gutachtal (D) 1991 (dessin : J. Spelda) ; E : *R. m. cervina*, Pratteln (CH) 1910, Zoologische Staatssammlung München ; F : *R. m. cervina*, Küssnach (D) 1990 (dessin : J. Spelda) ; G : *R. m. alemannica*, Staad (CH) 1916, Zoologische Staatssammlung München ; H : *R. m. alemannica*, Badenweiler 1990 (D) (dessin : J. Spelda).

FIG. 1. — Cheirites and colpocoxites of: A: R. m. montivaga, *Mauborget (CH) 1990 (drawning: J. Spelda); B:* R. m. wehrana, *Hasel (D) 1991 (drawning: J. Spelda); C:* R. m. serrata, *Inzlingen (D) 1990 (drawning: J. Spelda); D:* R. m. verhoeffi, *Hornberg, Gutachtal (D) 1991 (drawning J. Spelda); E:* R. m. cervina, *Pratteln (CH) 1910, Zoologische Staatssammlung München; F:* R. m. cervina, *Küssnach (D) 1990 (drawning: J. Spelda); G:* R. m. alemannica, *Staad (CH) 1916, Zoologische Staatssammlung München; H:* R. m. alemannica, *Badenweiler 1990 (D) (drawning: J. Spelda).*

Source : MNHN, Paris

b) *aelleni*

Ce taxon a été décrit par SCHUBART sur la base d'un seul mâle en provenance d'une grotte près de Baar. Aucune autre station n'est connue. Nous avons récolté dans les environs immédiats de cette grotte (station 54) 17 mâles et 10 femelles. La morphologie de ces individus, de même que les figures de *aelleni* dessinées par SCHUBART, entrent dans les variations observées pour *cervina*. Par ailleurs, les individus de Baar ne présentent aucune différence génétique avec les *cervina* en provenance de Suisse (Table 1, Part 1).

Nous proposons donc de considérer *aelleni* comme synonyme de *cervina*.

c) *alemannica* (Fig. 1 G, H)

Ce taxon se caractérise, selon VERHOEFF (1910 & 1916) par :

- une corne rostrale courte au syncolpocoxite (comme chez *serrata*)
- la courbe de la lame à faucille divisée en deux par une dent triangulaire
- le haut et le bas du prolongement basal du cheirite en général non resserré et sa pointe dressée et courte.

La différenciation des variétés décrites pour *alemannica* (*globosum, triarticulatum*) se base sur des critères variables, tels les télopodites des paragonopodes. La variabilité de ces pièces a déjà été soulignée antérieurement pour *montivaga* par exemple (PEDROLI-CHRISTEN, 1990). Si les populations en provenance de France, d'Ajoie et de Badenweiler ne posent pas de problème de détermination, d'autres populations, ou certains individus parmi elles, sont difficilement distinguables de *cervina* (26, 27, 53 ; Table 1, Part 1), un ou plusieurs caractères se rapprochant ou se confondant avec les caractères de *cervina*.

d) *verhoeffi* (Fig. 1 D)

Du point de vue morphologique, ce taxon occupe une position intermédiaire entre *cervina* et *wehrana*. Selon VERHOEFF (1916), la corne rostrale du syncolpocoxite égale ou dépasse la longueur de la lame en faucille et est droite ou recourbée vers le haut. Sur la courbure apicale du cheirite il peut y avoir une petite dent. La base du prolongement basal présente vers l'arrière une gibbosité. Ce taxon a été identifié sans problème dans deux localités (station 42, 43, Table 1, Part 1), ailleurs (stations 34 et 49, Table 1, Part 1), une séparation nette par rapport à *cervina* et *wehrana* est plus difficile.

D'une manière générale, on constate donc pour tous les taxons une variabilité morphologique relativement importante, pouvant engendrer des difficultés de diagnostic car la limite entre deux taxons morphologiques est, dans certains cas, floue. Les populations problématiques sont souvent situées dans les régions où les résultats enzymatiques montrent des transitions entre groupes de populations génétiquement différenciés.

DISCUSSION

Les nombreux taxons du genre *Rhymogona* ont été décrits au début de ce siècle au moment où la myriapodologie connaissait un grand essor dans la région. La systématique était alors exclusivement basée sur le concept typologique de l'espèce. Selon l'ampleur des variations observées, de nouvelles sous-espèces ou espèces (morphologiques) étaient alors décrites à la moindre différence. Si la classification typologique est un outil de travail facilement utilisable dans la pratique et appliqué, selon MAYR (1967), au début de toutes recherches scientifiques d'un groupe, elle n'est aujourd'hui plus d'actualité. Les résultats de cette étude des populations appellent à suivre le concept biologique de l'espèce, définie comme un groupe de populations se reproduisant entre elles, mais qui est toutefois reproductivement isolé d'autres groupes de populations (MAYR, 1967). En fonction des résultats obtenus, particulièrement l'arrangement géographique des populations génétiquement différenciées, nous proposons de considérer *Rhymogona* comme un genre monospécifique et l'unique espèce du genre comme une espèce polytypique. Les différentes "espèces morphologiques" doivent alors être traitées comme des sous-espèces :

Source : MNHN, Paris

Genus *Rhymogona* Cook, 1896

Rhymogona Cook, 1896 Espèce-type : *Atractosoma montivaga* Verhoeff 1894
Macheiriophoron Verhoeff, 1897 Espèce-type : *Atractosoma montivaga* Verhoeff 1894

Rhymogona montivaga (Verhoeff, 1894)

Rhymogona montivaga montivaga (Verhoeff, 1894)

1894 *Atractosoma montivagum* Verhoeff
1899 *Macheiriophoron montivagum silvaticum* Rothenbühler
1910 *Macheiriophoron silvaticum* Verhoeff
1990 *Rhymogona silvatica* Pedroli-Christen
1990 *Rhymogona montivaga* Pedroli-Christen et Scholl
1991 *Rhymogona montivaga* Pedroli-Christen et Scholl
1993 *Rhymogona montivaga* Pedroli-Christen

R. montivaga hessei (Brolemann, 1935)

1935 *Macheiriophoron montivagum hessei* Brolemann
1942 *Macheiriophoron montivagum hessei* Ravoux
1959 *Macheiriophoron montivagum hessei* Demange

R. montivaga cervina (Verhoeff, 1910)

1910 *Macheiriophoron cervinum* Verhoeff
1913 *Macheiriophoron cervinum* Bigler
1915 *Macheiriophoron cervinum* Verhoeff
1916 *Macheiriophoron cervinum* Verhoeff
1916 *Macheiriophoron cervinum var. brevidentatum* Verhoeff
1934 *Macheiriophoron cervinum* Schubart
1936 *Macheiriophoron cervinum* Verhoeff
1960 *Macheiriophoron aelleni* Schubart (syn. nov.)
1990 *Rhymogona cervina* Pedroli-Christen
1991 *Rhymogona cervina* Pedroli-Christen et Scholl
1991 *Rhymogona cervina* Spelda
1993 *Rhymogona cervina* Pedroli-Christen

R. montivaga alemannica (Verhoeff,1910)

1910 *Macheiriophoron alemannicum* Verhoeff
1913 *Macheiriophoron alemannicum* Bigler
1913 *Macheiriophoron alemannicum* var. *globosum* Bigler
1913 *Macheiriophoron alemannicum* var. *triarticulatum* Bigler
1913 *Macheiriophoron alemannicum* Verhoeff
1916 *Macheiriophoron alemannicum genuinum* Verhoeff
1916 *Macheiriophoron alemannicum rotundatum* Verhoeff
1916 *Macheiriophoron alemannicum* var. *triarticulatum* Verhoeff
1934 *Macheiriophoron alemannicum* Schubart
1935 *Macheiriophoron alemannicum* Verhoeff
1983 *Macheiriophoron alemannicum* Kobel-Voss
1991 *Rhymogona alemannica* Spelda
1993 *Rhymogona alemannica* Pedroli-Christen

Source : MNHN, Paris

R. montivaga verhoeffi (Bigler 1913)
1913 *Macheiriophoron verhoeffi* Bigler
1916 *Macheiriophoron verhoeffi genuinum* Verhoeff
1916 *Macheiriophoron verhoeffi excavatum* Verhoeff
1991 *Rhymogona verhoeffi* Spelda

R. montivaga serrata (Bigler, 1913)
1913 *Macheiriophoron serratum* Bigler
1991 *Rhymogona serrata* Spelda

R. montivaga wehrana (Verhoeff, 1910)
1910 *Macheiriophoron wehranum* Verhoeff
1916 *Macheiriophoron wehranum genuinum* Verhoeff
1916 *Macheiriophoron wehranum calcivagum* Verhoeff
1935 *Macheiriophoron wehranum genuinum* Verhoeff
1935 *Macheiriophoron wehranum quadridentatum* Verhoeff
1935 *Macheiriophoron wehranum clavigerum* Verhoeff
1936 *Macheiriophoron wehranum* Verhoeff
1991 *Rhymogona wehrana* Spelda

REMERCIEMENTS

Nous tenons à remercier vivement Jörg SPELDA pour sa collaboration sur le terrain et pour les dessins mis à notre disposition, ainsi que le Dr. Henrik ENGHOFF et Yves GONSETH pour la lecture critique du manuscrit. Nos remerciements vont également au Dr. H. FECHTER, Zoologische Staatssammlung München et au Dr. M. BRANCUCCI, Naturhistorisches Museum Basel, pour le prêt de matériel de collection. L'Académie Suisse des Sciences, qui a accordé une allocation pour les recherches sur le terrain en Allemagne et en France, mérite aussi notre gratitude.

RÉFÉRENCES

BIGLER, W., 1913. — Die Diplopoden von Basel und Umgebung. *Rev. suisse Zool.*, **21** : 675-793.

BROLEMANN, H., 1935. — Faune de France 29. Myriapodes Diplopodes (Chilognathes I). Paris, P. Lechevalier, 1-369.

COOK, O. F., 1896. — II. On recent diplopod names. *Brandtia* : 5-8.

DEMANGE, J.-M., 1959. — Myriapodes des cavités de la Côte d'Or, de la Saône-et-Loire et du Jura. *Sous le Plancher*, **2** : 32-35.

HOFFMAN, R. L., 1980. — *Classification of the Diplopoda*. Genève, Muséum d'Histoire naturelle, (1979), 237 pp.

KOBEL-VOSS, A., 1983. — Zur Isopoden- und Diplopodenfauna des Naturschutzgebietes "Mindelsee". [*In* : *Der Mindelsee bei Radolfzell*.] *Natur- u. Landschaftschutzgebiete Bad.-Württ.*, **11** : 531-538.

MAYR, E., 1967. — *Artbegriff und Evolution (dtsch. Übersetzung von Animal, Species and Evolution)*. Hamburg, Berlin, 617 pp.

PEDROLI-CHRISTEN, A., 1990. — Field investigations on *Rhymogona cervina* Verhoeff and *Rhymogona silvatica* Rothenbühler (Diplopoda): Morphology, distribution and hybridisation. *In* : A. MINELLI, *Proc. 7th int. Congr. Myriapodology* , Leiden, E. J. Brill : 27-43.

PEDROLI-CHRISTEN, A., 1993. — Faunistique des Mille-pattes de Suisse (Diplopoda) / Faunistik der Tausendfüssler der Schweiz (Diplopoda). Neuchâtel, Centre Suisse de Cartographie de la faune, Doc. faun. helv., **14**, 1-248.

PEDROLI-CHRISTEN, A. & SCHOLL, A., 1990. — Ecological and genetic studies on parapatric *Rhymogona silvatica* (Roth.) and *R. cervina* (Verh.) (Diplopoda: Craspedosomatidae) with special reference to hybrid populations in a zone of contact. *Rev. suisse Zool.*, **97** : 349-359.

PEDROLI-CHRISTEN, A. & SCHOLL, A., 1991. — Systématique et taxonomie du genre *Rhymogona* (Diplopoda: Craspedosomatidae): *Rhymogona silvatica* (Rothenbühler, 1899) synonyme de *Rhymogona montivaga* (Verhoeff,1894); résultats morphologiques et génétiques. *Rev. suisse Zool.*, **98** : 83-92.

RAVOUX, P., 1942. — Description de la femelle de *Macheiriophoron silvaticum hessei*. *Arch. Zool. exp. & gén.*, **82** : 91-99.

ROTHENBÜHLER, H., 1899. — Ein Beitrag zur Kenntnis der Diplopodenfauna der Schweiz I. *Rev. suisse Zool.*, **6** :199-271.

Source : MNHN, Paris

SCHUBART, O., 1934. — Tausendfüssler oder Myriapoda I. Diplopoda. *In* : F. DAHL, *Tierw. Deutschl.* **28** Jena, G. Fischer, 318 pp.

SCHUBART, O., 1960. — Über einige Höhlen-Diplopoden der Schweiz und Frankreichs. *Rev. suisse Zool.*, **67** : 561-588.

SPELDA, J., 1991. — Zur Faunistik und Systematik der Tausendfüssler (Myriapoda) Südwestdeutschlands. *Jh. Ges. Natur. Württ.*, **146** : 211-232.

VERHOEFF, K. W., 1894. — Beiträge zur Diplopodenfauna der Schweiz. *Berl. entom. Z.*, **39** : 281-296.

VERHOEFF, K. W., 1897. — Übersicht der mir genauer bekannten Europaïschen Chordeumiden-Gattungen (Beiträge zur Kenntnis paläarktischer Myriopoden 5). *Arch. f. Naturg.*, **63** : 129-138.

VERHOEFF, K. W., 1910. — Über Diplopoden. Deutsche Craspedosomiden. *Sitz.ber. Ges. naturforsch. Freunde Berlin* : 19-62.

VERHOEFF, K. W., 1913. — Die weiblichen Fortpflanzungswerkzeuge von *Listocheiritium* und *Macheiriophoron*. *Zool. Anz.*, **41** : 398-409.

VERHOEFF, K. W., 1915. — Beiträge zur Kenntnis der Diplopoden von Württemberg, Hohenzollen und Baden. *Jh. Ver. vaterl. Naturk. Württemberg* , **71** : 1-54

VERHOEFF, K. W., 1916. — Beiträge zur Kenntnis der Gattung *Macheiriophoron* und *Craspedosoma*. *Zool. Jb.*, **39** : 273-416.

VERHOEFF, K. W., 1935. — Quer durch Schwarzwald und schweizerischen Jura. *Verh. naturwiss. Ver. Karlsruhe*, **31** : 153-174.

VERHOEFF, K. W., 1936. — Unsere Kenntnis von den Diplopoden des alemannischen Gaues. *Ber. naturf. Ges. Freiburg*, **35** : 162-195.

Source : MNHN, Paris

Mastigophorophyllon (Verhoeff, 1897) et *Karpatophyllon* Jawlowsky, 1928 : genres carpatiques (Chordeumatida, Diplopoda)

***Traian* CEUCA**

Universitatea din Cluj-Napoca, Facultatea de Biologie, Catedra de Zoologie, str. Clinicilor 5-7
RO-3400 Cluj-Napoca, Roumanie

RÉSUMÉ

Le genre *Mastigophorophyllon* comprend en général des formes de haute altitude vivant surtout dans les prairies alpines, parfois à la lisière des forêts de conifères et plus rarement à celle des forêts de feuillus. Sur les six espèces dépourvues de rameau plumiforme sur la partie postérieure des gonopodes antérieurs, cinq sont répandues uniquement dans les Carpates Méridionales ; ce sont : *M. alpivagum*, *M. deubeli*, *M. transsilvanicum*, *M. carpaticum* et *M. banarescui*. La seule espèce située en dehors de l'aire carpatique est *M. bohemicum*, répartie en Bohême. Sur les dix formes comportant un rameau plumiforme sur la partie postérieure des gonopodes antérieurs, huit sont cantonnées dans les Carpates du Nord et les Carpates Orientales ; ce sont : *M. penicilligerum*, *M. cirriferum*, *M. jickelii*, *M. serrulatum*, *M. s. apiculatum*, *M. crinitum*, *M. c. huculicum*, *M. aberratum* et *M. saxonicum*. Deux autres formes se rencontrent en Bulgarie (Monts Balkans) : *M. bulgaricum* et *M. b. pirinicum*. Le genre *Karpatophyllon* renferme seulement quatre espèces : *K. polinskii*, *K. dacicum*, *K. carpaticum* et *K. banaticum*. Elles sont répandues dans une aire qui relie les Carpates du Nord-Est aux Carpates Méridionales, par l'intermédiaire des Monts Apuseni et des Monts Poiana Ruscai ; cette répartition circonscrit l'ensemble du Plateau de Transylvanie. On peut affirmer que les genres *Mastigophorophyllon* et *Karpatophyllon* sont bien liés, d'un point de vue géographique, à la Chaîne carpatique.

ABSTRACT

***Mastogophorophyllon* (Verhoeff, 1897) *and Karpatophyllon* Jawlowsky, 1928, Carpathian genera (Chordeumatida, Diplopoda)**

The genus *Mastigophorophyllon* comprises of forms living at high altitudes, especially in prealpine areas, sometimes on the edge of coniferous woods but seldom on the edge of deciduous woods. Among the six species showing no "featherlike" branches on the posterior part of the anterior gonopods, five are found only in the meridional Carpathian Mountains, these being: *M. alpivagum*, *M. deubeli*, *M. transsilvanicum*, *M. carpaticum* and *M. banarescui*. The only species found outside of the Carpathian area is from Bohemia. Ten forms have a "featherlike" branch at the posterior part of the anterior gonopods, eight of them being distributed in the Northern and Eastern Carpathians: *M. penicilligerum*, *M. cirriferum*, *M. jickelii*, *M. serrulatum*, *M. s. apiculatum*, *M. crinitum*, *M. c. huculicum*, *M. aberratum* and *M. saxonicum*. Species belonging to the genus *Karpatophyllon* seem to prefer deciduous woods reaching upwards to the lower limit of coniferous forests. Only four species belong to this genus. They are distributed in an area that links the North-Eastern to the Southern Carpathians (Apuseni and Poina Ruscai Mounts). These species are: *K. polinski*, *K. dacicum*, *K. carpaticum* and *K. banaticum*. We may say that the two genera *Mastigophorophyllon* and *Karpatophyllon* are geographically connected to the Carpathian Mountains.

CEUCA, T., 1996. — *Mastigophorophyllon* (Verhoeff, 1897) et *Karpatophyllon* Jawlowsky, 1928, genres des Carpates (Chordeumatida, Diplopoda). *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 61-65. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

INTRODUCTION

Les deux genres qui font l'objet de notre analyse constituent, avec quelques autres, la famille des Mastigophorophyllidae, et se distinguent nettement, tant du point de vue morphologique (notamment par l'aspect des gonopodes) que du point de vue géographique, des espèces se répartissant en Europe centrale et orientale. Le genre *Mastigophorophyllon* comprend des formes vivant généralement en haute altitude, surtout dans les prairies alpines, parfois à la lisière des forêts de conifères et plus rarement à celle des forêts de feuillus. On les trouve dans la litière, au bord des sentiers ou des routes forestières. Certaines espèces se rencontrent de préférence, dans les prairies alpines, sous les touffes d'herbe ou autour des quelques rares conifères présents. Pendant les périodes de sécheresse prolongée, elles recherchent l'humidité que conservent les branches de genévrier étendues au ras du sol (cf. STOJALOWSKA, 1961 ; TABACARU, 1990 ; VERHOEFF, 1900).

RÉSULTATS

Dans un travail publié en 1976 sur le genre *Mastigophorophyllon*, j'ai montré que les deux sections créées par VERHOEFF, sur la base de la présence ou de l'absence d'un rameau plumiforme sur la partie postérieure des gonopodes antérieurs, peuvent avoir valeur de sous-genres. Notons que cinq des six espèces du sous-genre *Mastigophorophyllon* dépourvues de ce rameau sont uniquement distribuées dans les Carpates méridionales (Alpes de Transylvanie) ; ce sont :

Mastigophorophyllon (M.) alpivagum (Verhœff, 1897) des Monts de Cindrel.
Mastigophorophyllon (M.) deubeli Verhœff, 1898 des Monts de Bucegi.
Mastigophorophyllon (M.) transsilvanicum Attems, 1900 des Monts de Bucegi.
Mastigophorophyllon (M.) carpaticum Ceuca, 1976 des Monts de Retezat (FIG. 1A).
Mastigophorophyllon (M.) banarescui Ceuca, 1976 des Monts de Retezat.

Ces endémismes peuvent être dus à la fragmentation de la chaîne carpatique par des vallées transversales, dont le résultat est l'isolement paléogéographique, sous forme d'îlots, des zones de haute altitude. Beaucoup d'autres diplopodes strictement localisés, ainsi que des espèces endémiques fort diverses, doivent avoir d'ailleurs la même origine.

La seule espèce connue en dehors de cette aire carpatique, est *M. (M.) bohemicum* Attems, habitant la Bohême (ATTEMS, 1900) ; sa présence dans une région aussi éloignée est difficilement explicable.

Une distribution tout aussi étroitement délimitée caractérise le second sous-genre, *Paramastigophorophyllon* (pourvu de rameau plumiforme), dont huit des dix formes connues sont cantonnées dans les Carpates du Nord et les Carpates Orientales. Ce sont :

Mastigophorophyllon (P.) penicilligerum Verhœff, 1899 des Monts Rodna.
Mastigophorophyllon (P.) cirriferum Verhœff, 1899 des Monts de Tatra.
Mastigophorophyllon (P.) jickelii Verhœff, 1900 de Borsec.
Mastigophorophyllon (P.) serrulatum Attems, 1926 des Monts Rarau.
Mastigophorophyllon (P.) s. apiculatum Jawlowski, 1935 des Carpates de l'Ukraine.
Mastigophorophyllon (P.) crinitum Attems, 1926 de Virghis.
Mastigophorophyllon (P.) c. huculicum Jawlowski, 1935 des Carpates de l'Ukraine.
Mastigophorophyllon (P) aberratum Ceuca, 1985 des Monts de Rodna.

La position zoogéographique de *M. (P.) bulgaricum* Schubart, 1939, et de sa sous-espèce *M. (P.) b. pirinicum* est très intéressante (GULICKA, 1967). On trouve les deux formes dans les Balkans, à la limite sud de la répartition du genre *Mastigophorophyllon* , alors qu'il n'y a aucun représentant du sous-genre *Paramastigophorophyllon* le long des Carpates méridionales.

La seule espèce qui occupe une aire très vaste, dépassant largement l'aire carpatique, est *M. (P.) saxonicum* Verhœff, 1916. Elle est fréquente en Allemagne, où elle a été trouvée dans

Source : MNHN, Paris

de nombreuses localités (SCHUBART, 1934), certaines probablement de faible altitude ; elle a été également signalée en Lettonie, Estonie, Pologne, Slovaquie, dans l'ouest de l'Ukraine et en Roumanie (dans les Carpates du nord du pays). Avec une aussi large répartition, il semble naturel de constater, chez cette espèce, une certaine variabilité de la morphologie des gonopodes, d'autant plus marquée que les individus proviennent des confins orientaux et occidentaux de son aire géographique, ce qui peut être interprété comme une distribution le long d'un cline.

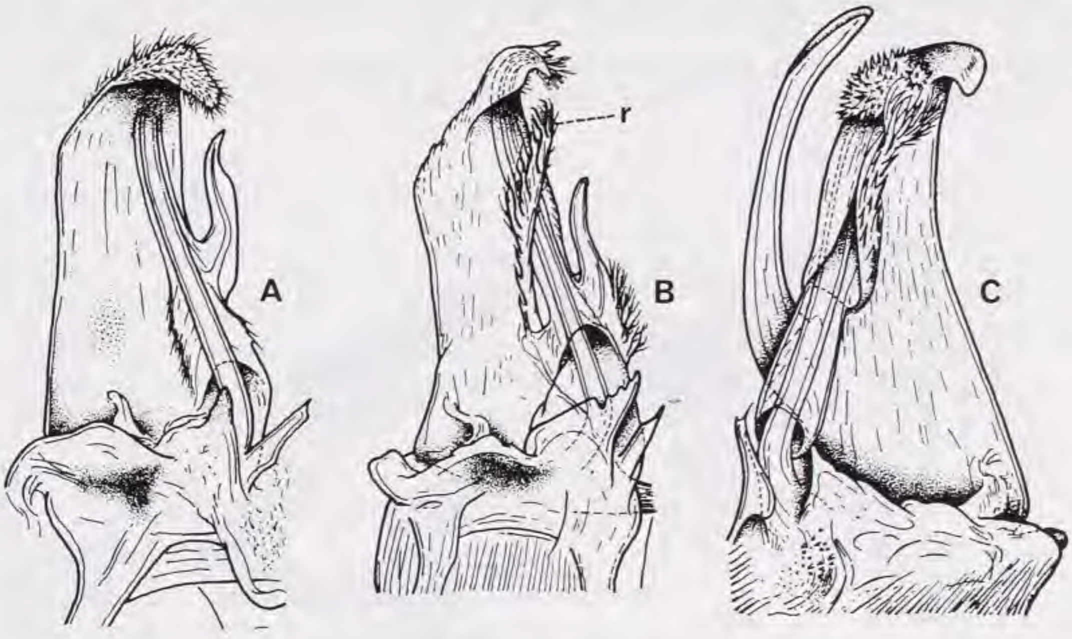


FIG. 1. — A : exemple de gonopode antérieur sans rameau plumiforme sur la face postérieure, *M. (M.) carpaticum* ; B : gonopode antérieur avec rameau plumiforme (r.), *M. (P.) serrulatum* ; C : gonopode antérieur, en vue postérieure, de *K. dacicum*. (d'après ATTEMS, 1926 ; CEUCA, 1964, 1976).

FIG. 1. — A: anterior gonopod without "feather-like" branch on the posterior side, M. (M.) carpaticum *; B: anterior gonopod with "feather-like' branch (r),* M. (P.) serrulatum*; C: anterior gonopod, posterior view,* K. dacicum.

Dans le travail déjà mentionné ci-dessus (CEUCA, 1976), j'ai soutenu que le genre *Mastigophorophyllon* faisait défaut dans les Monts Apuseni situés en Transylvanie, à l'intérieur de l'arc carpatique. J'ai cependant identifié, à la demande d'un collègue, des restes de diplopodes, plus ou moins digérés, trouvés dans l'estomac d'un lézard (*Lacerta vivipara*) capturé dans les Monts Apuseni. Parmi les débris figurait un septième anneau comprenant des gonopodes intacts pouvant appartenir à *M. (P.) saxonicum*. Des recherches ultérieures effectuées dans les mêmes montagnes m'ont fourni des exemplaires capturés dans trois autres stations. Les particularités morphologiques de leurs gonopodes pourraient justifier la création d'une sous-espèce nouvelle dont l'étude constituera le sujet d'un travail particulier. Il faut également remarquer que les stations en question se situent à la lisière de forêts situées à de plus basses altitudes et constituées d'un mélange de conifères et de feuillus.

En ce qui concerne le troisième sous-genre, *Metamastigophorophyllon*, dont la seule espèce connue actuellement est *M. (M.) giliarovi* Lang, 1959 du Caucase (Krasnaia Poliana), une révision détaillée de la morphologie externe et des gonopodes paraît nécessaire afin de démontrer son appartenance au genre *Mastigophorophyllon* .

L'autre genre qui fait l'objet de notre attention, *Karpatophyllon*, a été créé par JAWLOWSKY en 1928 lors de la description de *K. polinskii*, espèce découverte en Ukraine

Source : MNHN, Paris

(Podolie, Collines du Prut) et retrouvée, plus tard, dans trois stations des Carpates du nord de la Roumanie (Monts de Rodna). Ce genre renferme à ce jour trois autres espèces, réparties, elles aussi, dans le périmètre carpatique :

Karpatophyllon polinskii Jawlowski, 1928, Ukraine et Monts Rodna.
Karpatophyllon dacicum Ceuca, 1964, des Monts Apuseni (Fig. 1C).
Karpatophyllon carpaticum Ceuca, 1985 des Monts du Lapus.
Karpatophyllon banaticum Ceuca, 1989 des Monts Poiana Ruscäi.

De ce qui précède, il s'ensuit que la répartition géographique du genre *Karpatophyllon* permet de relier les Carpates du Nord-Est aux Carpates méridionales par l'intermédiaire des Monts Apuseni et des Monts Poiana Ruscäi, ces derniers flanquant vers le Nord-Ouest les Monts de Retezat ; on voit donc cette répartition circonscrire le Plateau de la Transylvanie, du côté Ouest (Fig. 2).

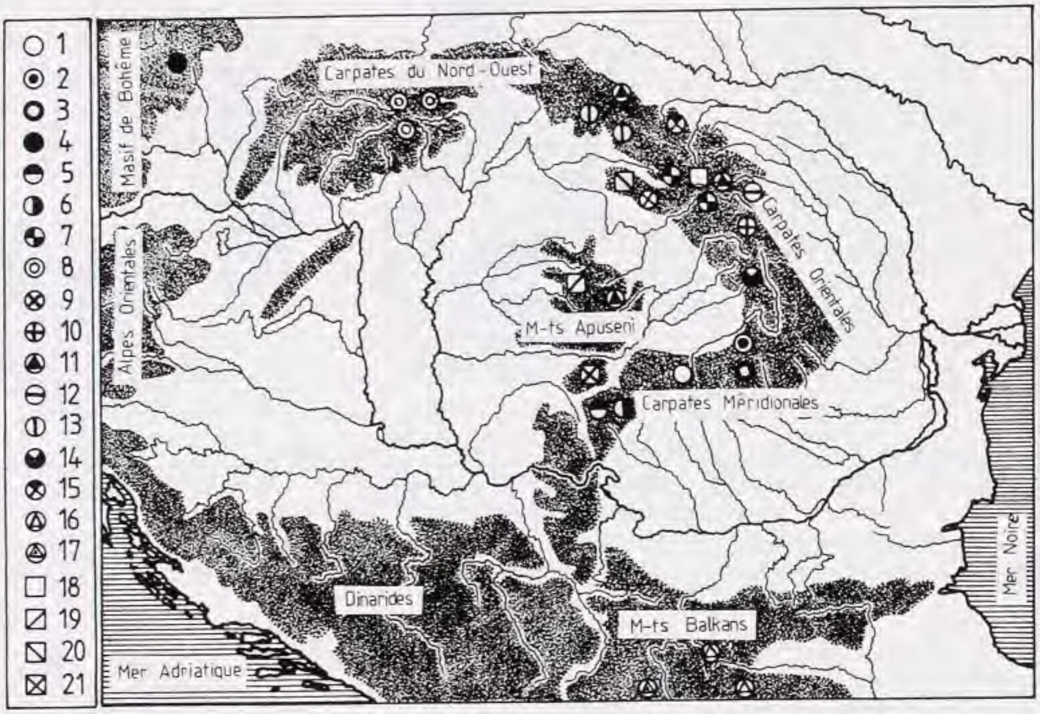


FIG. 2. — Répartition des genres *Mastigophorophyllon* et *Karpatophyllon*. 1 : *M. (M.) alpivagum* ; 2 : *M. (M.) deubeli* ; 3 : *M. (M.) transsilvanicum* ; 4 : *M. (M.) bohemicum* ; 5 : *M. (M.) carpaticum* ; 6 : *M. (M.) banaticum* ; 7 : *M. (P.) penicilligerum* ; 8 : *M. (P.) cirriferum* ; 9 : *M. (P.) aberratum* ; 10 : *M. (P.) jickelii*; 11 : *M. (P.) saxonicum* ; 12 : *M. (P.) serrulatum* ; 13 : *M. (P.) s. apiculatum* ; 14 : *M. (P.) crinitum* ; 15 : *M. (P.) c. huculicum* ; 16 : *M. (P.) bulgaricum* ; 17 : *M. (P.) b. pirinicum* ; 18 : *K. polinskii* ; 19 : *K. dacicum* ; 20 : *K. carpaticum* ; 21 : *K. banaticum*.

FIG. 2. — Distribution of the genera Mastigophorophyllon *and* Karpatophyllon. *1:* M. (M.) alpivagum*; 2:* M. (M.) deubeli*; 3:* M. (M.) transsilvanicum*; 4:* M. (M.) bohemicum*; 5:* M. (M.) carpaticum*; 6:* M. (M.) banaticum*; 7:* M. (P.) penicilligerum*; 8:* M. (P.) cirriferum*; 9:* M. (P.) aberratum*; 10:* M. (P.) jickelii*; 11:* M. (P.) saxonicum*; 12:* M. (P.) serrulatum*; 13:* M. (P.) s. apiculatum*; 14:* M. (P.) crinitum*; 15:* M. (P.) c. huculicum*; 16:* M. (P.) bulgaricum*; 17:* M. (P.) b. pirinicum*; 18:* K. polinskii*; 19:* K. dacicum*; 20:* K. carpaticum*; 21:* K. banaticum.

Les espèces du genre paraissent préférer les forêts de feuillus, s'élevant en altitude jusqu'à la limite inférieure des forêts de conifères.

Source : MNHN, Paris

CONCLUSION

On peut affirmer que les genres *Mastigophorophyllon* et *Karpatophyllon* sont liés, du point de vue géographique, à la chaîne carpatique d'où ils sont issus, se sont diversifiés et ont étendu leur aire de répartition. Il apparaît également que la présence ou l'absence du rameau plumiforme des gonopodes antérieurs chez *Mastigophorophyllon* n'a pas dû jouer un rôle très important.

RÉFÉRENCES

ATTEMS, C., 1900. — Ueber der Färbung von *Glomeris* und Beschreibung neuer oder weniggekanter Myriopoden. *Arch. Naturg.*, **LXVI** : 313-316.

ATTEMS, C., 1926. — Über paläarktischer Diplopoden. *Arch. Naturg., Abt. A. H.*, **1-2** : 82-108.

CEUCA, T., 1959. — Genurile *Karpatophyllon* si *Stenophyllum* în fauna de Diplopode a României. *Stud. Univ. B. B. ser. Biol.*, **XXXIV** : 52-56.

CEUCA, T., 1964. — Cîteva Diplopode noi în fauna RPR. *Stud. Univ. B. B. ser. Biol.*, **XXXIX** : 89-92.

CEUCA, T., 1976 — Genul *Mastigophorophyllon* Verh. 1897 (Diplopoda-Ascospermophora). *Stud. Univ. B. B. ser. Biol.*, **LI** : 37-43.

GULICKA, J., 1967. — Neue und interessante Diplopoden aus Bulgarien. *Annotat. Zool. Bot.*, **39** : 1-3.

JAWLOWSKY, H., 1928. — *Karpatophyllum polinskii* n. sbg. n. sp., *Leptoiulus czarnohoricus* n. sp. (Diplop.). *Ann. Mus. Zool. Polonici*, **7** : 102-106.

SCHUBART, O., 1934. — Tausendfüssler oder Myriapoda I. Diplopoda. *In* : F. DAHL, *Tierw. Deutschl.* **28**, Jena, G. Fischer, 1-318.

STOJALOWSKA, W., 1961. — *Krocionogi (Diplopoda) Polski*. Warszawa, Polska Akademia Nauk: 216 pp.

TABACARU, I., 1969 (1970). — Sur l'origine de la faune des Diplopodes des Carpates. *Bull. Mus. natl. Hist. nat.*, **41** : 139-143.

VERHOEFF, K. W., 1900. — Beiträge zur Kenntnis paläarktischer Myriapoden. *Arch. Naturg.*, **LXVI** : 368-369.

Source : MNHN, Paris

Source : MNHN, Paris

Sur la remarquable conformation des apophyses génitales mâles chez un polydesmide néotropical

Ionel TABACARU

Institut de Spéologie "Emile Racovitza" Str. Frumoasa Nr. 11, RO-78114 Bucuresti , Roumanie

RÉSUMÉ

Description d'un genre nouveau de diplopodes, *Venezuelodesmus* n. g. (Trichopolydesmoidea, Fuhrmannodesmidae, Venezuelodesmini n. trib.), représenté par trois espèces (*V. orghidani* n. sp., *V. decui* n. sp., *V. bordoni* n. sp.) trouvées au Venezuela, chez lesquelles les coxa de la deuxième paire de pattes sont modifiées en remarquables apophyses génitales portant des télopodites réduits et surmontant un long organe musculeux évaginable.

ABSTRACT

On the noteworthy structure of male genital apophyses in a Neotropical polydesmid millipede.

Description of a new millipede genus, *Venezuelodesmus* n. g. (Trichopolydesmoidea, Fuhrmannodesmidae, Venezuelodesmini n. trib.) including three species (*V. orghidani* n. sp., *V. decui* n. sp., *V. bordoni* n. sp.) found in Venezuela and showing the coxae of the second pair of legs transformed into remarkable genital apophyses supporting reduced telopodites and overlying a long musculous evaginable organ.

INTRODUCTION

Il est bien connu que, chez les mâles de diplopodes polydesmides, les canaux déférents perforent dans leur longueur les coxae des pattes de la deuxième paire et débouchent à l'extérieur chacun par un gonopore situé à l'angle distal interne de la hanche. On utilise chez les diplopodes le nom de pénis mais je préfère utiliser dorénavant le nom d'apophyse génitale car, ainsi que l'a montré le biologiste français Albert VANDEL (1943) dans un cas parfaitement similaire, le nom de pénis est manifestement inexact : en effet, ces formations, constituées par la partie terminale des canaux déférents, avec les orifices génitaux à leur extrémité, ne jouent jamais le rôle d'organe d'intromission.

En tout cas, chez les polydesmides, il s'agit d'un simple entonnoir situé parfois sur une proéminence et entouré souvent de quelques soies (Fig. 1A). Cependant, en examinant des petites formes de polydesmides récoltées au Venezuela par le regretté professeur Traian ORGHIDAN, M. Carlos BORDON, de Caracas, et mon ami V. DECU, j'ai eu la surprise de trouver trois espèces nouvelles, appartenant à un genre nouveau, chez qui les coxae de la deuxième paire de pattes, porteuses de télopodites réduits, sont modifiées en de remarquables apophyses génitales. J'ai donné à ce genre le nom de *Venezuelodesmus* n. g. et aux trois nouvelles espèces

TABACARU, I., 1996. — Sur la remarquable conformation des apophyses génitales mâles chez un polydesmide néotropical. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 67-72. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

les noms respectifs de : *V. orghidani* n. sp., *V. bordoni* n. sp. et *V. decui* n. sp. (Figs. 1 & 2).

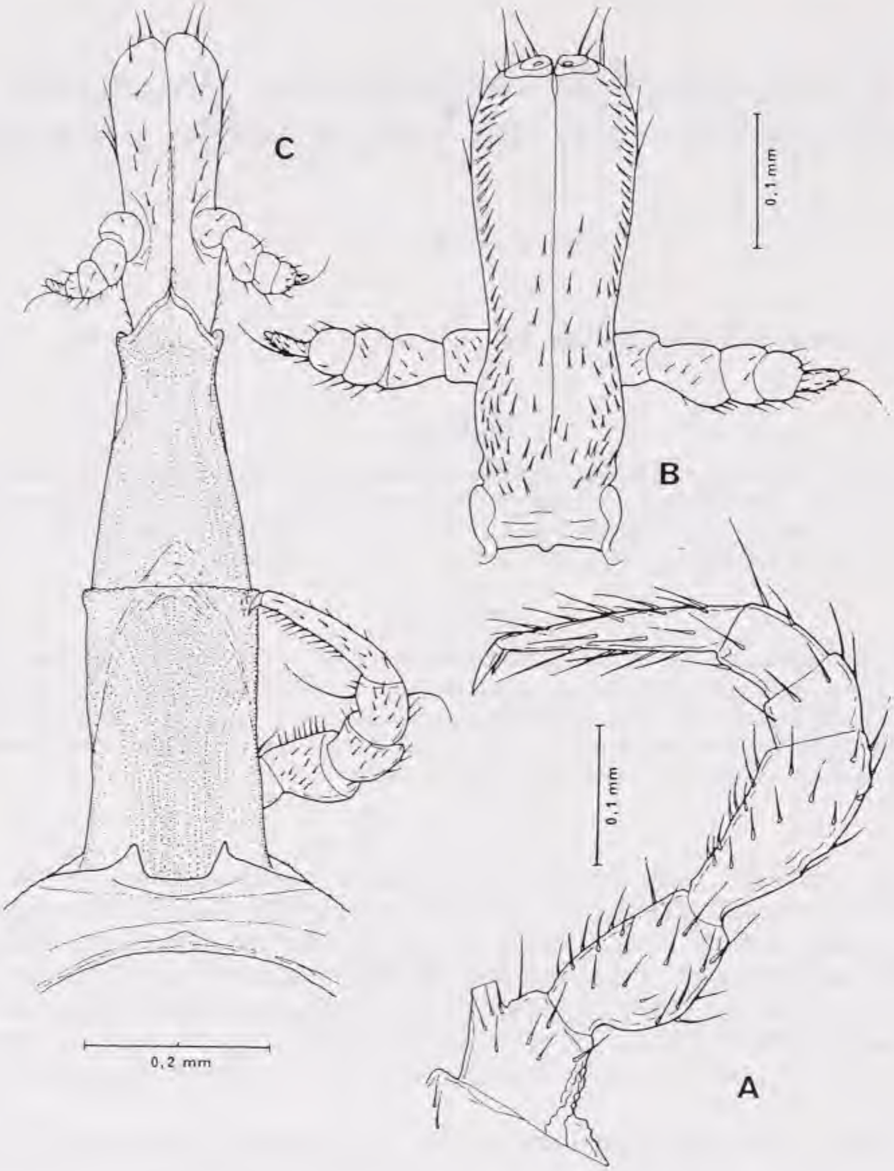


FIG. 1. — A. *Banatodesmus jeanneli* (Tabacaru, 1980), patte de la 2ème paire. B et C, *Venezuelodesmus decui* n. g., n. sp. : B, seconde paire de pattes ; C, la 2e paire de pattes sur l'organe musculeux évaginable.

FIG. 1. — A. Banatodesmus jeanneli *(Tabacaru, 1980), second pair of legs. B and C,* Venezuelodesmus decui *n. g., n. sp. : B: P2; C, P2 and musculous evaginable organ.*

Les trois espèces du genre *Venezuelodesmus* n. g. sont caractérisées par les hanches ou coxae, très longues et robustes de la 2ème paire de pattes. Ces coxae sont accolées et forment ensemble une languette légèrement élargie distalement et pourvue, sur la face orale, dans sa moitié proximale ainsi que le long de ses bords externes, de soies robustes dirigées vers l'apex. A l'apex, il y a quatre soies longues et plus robustes, surtout les deux latérales. Les deux coxae se terminent en crochets dirigés oralement et les orifices génitaux se trouvent à la base de ces

Source : MNHN, Paris

crochets. Sur chaque coxa, dans la moitié basale, face caudale, sont insérés les télopodites réduits de la 2ème paire de pattes. Ces télopodites sont constitués de six articles courts, surtout le dernier. L'avant-dernier article (le tibia) porte une très longue soie (Fig. 1B & C).

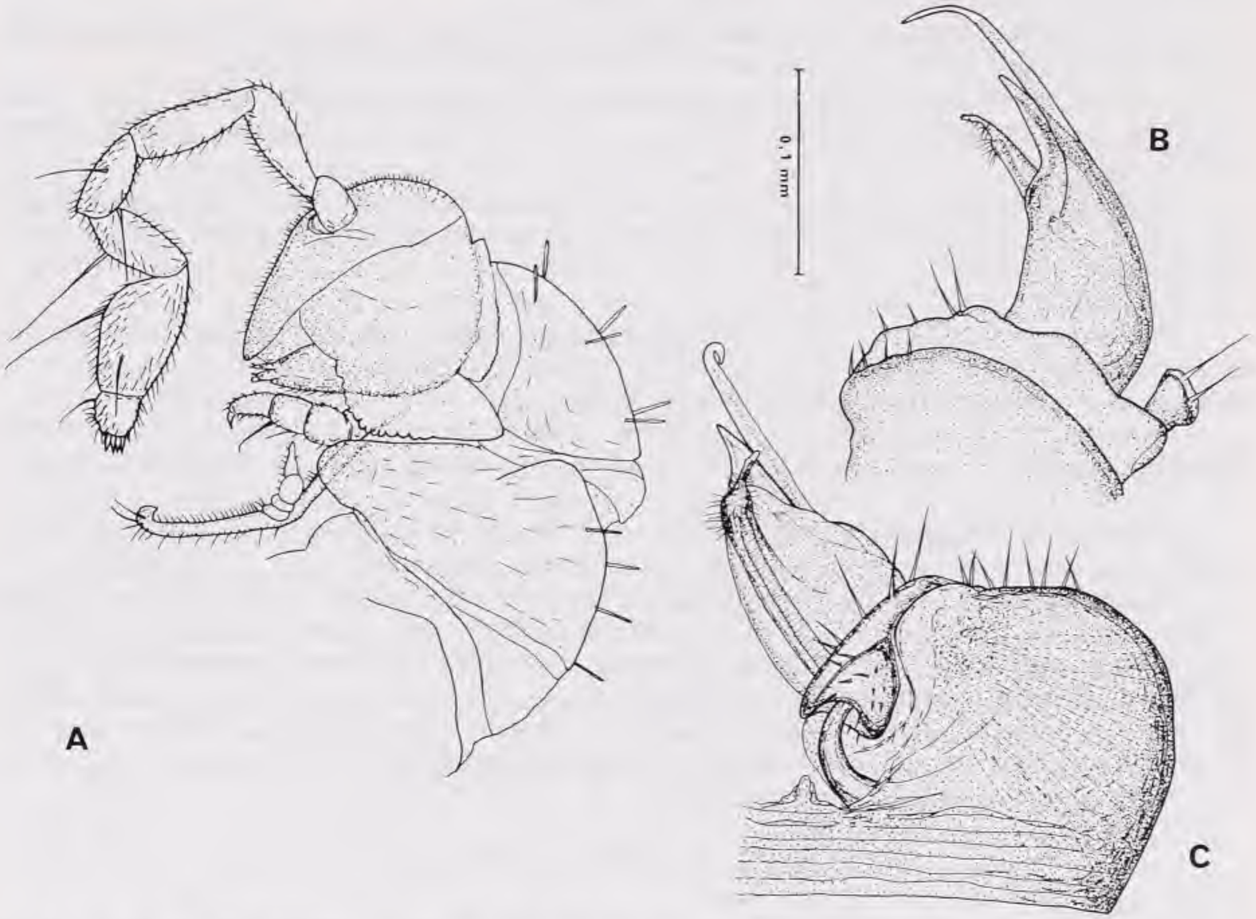


FIG. 2. — A. *Venezuelodesmus bordoni* n. sp., tête et les deux premiers tergites. B et C. *Venezuelodesmus decui* n. sp. : B, gonopode gauche, en vue externe ; C, gonopode gauche, en vue caudale.

FIG. 2. — A. Venezuelodesmus bordoni *n. sp., head and two first tergites. B and C.* Venezuelodesmus decui *n. sp.: B, left gonopod, external view; C, left gonopod, caudal view.*

Le sternite de la deuxième paire de pattes n'est pas soudé directement à l'arc pleuro-tergal du troisième segment car la languette constituée par les deux coxae accolées surmonte un organe allongé, très musculeux, à paroi membraneuse, qui présente une partie basale cylindrique et une partie distale en forme de tronc de cône. Cet organe musculeux appartient au troisième segment mais il s'évagine entre le bord du 2ème segment et le bord du 3ème segment. Le bord caudal de la partie ventrale du 2ème segment est profondément échancré et les lobes encadrant l'échancrure sont très saillants. L'organe musculeux évaginable est dirigé soit en avant, et dans ce cas les apophyses génitales dépassent la tête, soit en arrière, entre les pattes des segments suivants (Fig. 2A).

VENEZUELODESMUS N. G.

Polydesmida de taille très petite (5 - 5,5 mm) ; ♂ et ♀, 20 segments. Coloration complètement blanche ; téguments granuleux. Partie orale du corps non rétrécie.

Source : MNHN, Paris

Tête globuleuse. Antennes relativement longues ; 6ème antennomère nettement plus long que le 5ème. Labre tridenté ; mandibules prolongées vers la partie ventrale par une grande lamelle ovale, crênelée du côté antérieur ; gnathochilarium avec les stipes pourvus dans leur moitié basale de nombreuses soies robustes ; dans l'angle distal interne des lamelles linguales se trouvent deux styles à deux ou trois pointes émoussées.

Collum moins large que la tête, relativement long, de forme trapézoïdale, à angles arrondis et bords latéraux convexes, à surface garnie de trois rangées de soies claviformes.

Tergites convexes ; carènes peu saillantes à bords latéraux régulièrement arqués, sans denticulations ; surface des tergites avec trois rangées de soies claviformes. Limbe à dents courtes et pointues.

Le deuxième segment du ♂ est plus grand ; dans sa partie ventrale il est profondément échancré du côté caudal et les lobes encadrant l'échancrure sont très saillants ; pas de pore pleurotergal.

Formule des pores : 5, 7, 9, 10, 12, 13, 15-19.

Pattes sans denticulations sur les bords internes des articles. Première paire à tarse pourvu, sur le bord interne, d'un peigne de soies alignées plus fortes que les autres soies ; un groupe de fortes soies se trouve aussi sur la face orale du fémur.

Deuxième paire à sternite non soudé avec la partie ventrale du 3ème segment ; coxae immenses, accolées en une languette qui surmonte un long organe musculeux évaginable entre le 2ème et le 3ème segment ; télopodites réduits.

Dans la partie ventrale du 5ème segment, sur le sternite de la 5ème paire de pattes ou sur les sternites des 4ème et 5ème, il y a des processus portant des denticulations ou de longues épines.

Gonopodes : coxoïdes grands, globuleux ; les télopodites dirigés obliquement vers la ligne médiane s'entre-croisent. La zone préfémorale, en bourrelet pileux, est élargie dans la partie caudale où pénètre le crochet coxal. Le télopodite, profondément divisé, comprend d'une part, une branche tarsale, longue et grêle, recourbée vers l'arrière, et d'autre part une branche tibiale plus courte, arquée en faucille, à partie basale large ; de cette partie basale se détache la branche séminale. La rainure séminale est bien visible et son trajet est direct (Fig. 2B & C).

Espèce type du genre *Venezuelodesmus* n. g. : *V. decui* n. sp.

CLÉ DES TROIS ESPÈCES DE *VENEZUELODESMUS*

1 (2) Gonopodes : coxoïde pourvu d'une proéminence anguleuse au bord distal postérieur ; la région préfémoro-fémorale se prolonge en un lobe arrondi et aplati, connecté, par une lame, avec le solénomérite. Dans la partie ventrale du 5ème segment, sur le sternite des 4ème et 5ème paires de pattes, se trouve un grand processus en fer à cheval pourvu de denticulations .... *V. bordoni* n. sp.

Localité type : Parque National Rancho Grande (Henri Pittier) (Station 44 *in* DECU, BORDON & LINARES, 1987), 16-19. XI. 1982, 1000-1400 m, litière, 3 ♂♂, 2 ♀♀, leg. V. DECU, C. BORDON & T. ORGHIDAN.

2 (1) Gonopodes : coxoïde arrondi, sans proéminence anguleuse ; pas de prolongement fémoral. Dans la partie ventrale du 5ème segment il y a des processus qui n'ont pas la forme d'un fer à cheval .... 3.

3 (4) Gonopodes : les deux longues soies orales du coxoïde sont insérées dans une pièce en forme de coupe ; solénomérite sans éperon ; branche tarsale uniformément arquée à son extrémité. Dans la partie ventrale du 5ème segment, sur les sternites des 4ème et 5ème paires de pattes, se trouvent deux processus longitudinaux parallèles, pourvus de denticulations .... *V. decui* n. sp.

Localité type : Cerro La Pastora, Capadare, Edo Falcon (Station 51 *in* DECU, BORDON & LINARES, 1987), 13.XI.1982, Litière, 4 ♂♂, 6 ♀♀, leg. V. DECU & C. BORDON (dont 1 ♂ et 1 ♀ paratypes déposés au M.N.H.N. de Paris sous le n° JC 193).

Source : MNHN, Paris

4 (3) Gonopodes : les deux longues soies orales du coxoïde sont insérées sur la surface de celui-ci ; solénomérite pourvu d'un éperon pointu ; branche tarsale brusquement recourbée en crochet à son extrémité. Dans la partie ventrale du 5ème segment il y a un seul processus transversal sur le sternite de la 5ème paire de pattes, , pourvu de nombreuses et longues épines .... *V. orghidani* n. sp.

Localité type : Route vers la grotte Cueva del Tigre, Cerro la Passora, Edo Falcon, 12.XI.1982, 1 ♂, leg. T. ORGHIDAN.

SUR LA POSITION SYSTÉMATIQUE DU GENRE *VENEZUELODESMUS* N. G.

Le nouveau genre *Venezuelodesmus* n. g. fait partie d'un groupe de genres néotropicaux caractérisés par un habitus de type *Trichopolydesmus* et des gonopodes dont le coxoïde, très grand, enveloppe un télopodite condensé et de dimensions réduites (type cryptodesmoïde).

ATTEMS (1926, 1940) a rangé ces genres dans la famille des Vanhoeffeniidae Attems 1914 et on a longtemps considéré comme valable cette opinion. Cependant, JEEKEL (1965) a montré que ce nom de famille, en raison de son genre type, est synonyme de Sphaerotrichopidae Attems, 1914 et aussi de Dalodesmidae Cook, 1896.

VERHOEFF (1910, 1926-1932, 1941, 1942) a rangé ces genres dans la famille des Trichopolydesmidae Verhoeff, 1910 et cette position a été adoptée par KRAUS (1957, 1959, 1960), par LOOMIS (1964) et par SHEAR (1973). Dans des travaux relatifs aux représentants européens de la famille des Trichopolydesmidae (TABACARU, 1975, 1980), nous avons considéré cette famille dans le sens de VERHOEFF.

BRÖLEMANN (1916) a considéré que ces genres appartenaient à la famille des Cryptodesmidae Karsch, 1879 et les a classés à part dans la tribu des Fuhrmannodesmini Brölemann 1916. Cette opinion semble être soutenue par notre collègue MAURIÈS (1983) car il parle de "Cryptodesmides trichopolydesmiformes".

D'après HOFFMAN (1980) ces genres appartiennent à la famille des Fuhrmannodesmidae Brölemann, 1916, mais dans le cadre de la super-famille des Trichopolydesmoidea Verhoeff, 1910. Cette position a été soutenue par SIMONSEN (1990) dans son étude cladistique des Polydesmida. GOLOVATCH (1986) a aussi accepté la famille des Fuhrmannodesmidae.

Dans un travail concernant des Fuhrmannodesmidae de la région d'Amazonie (Brésil), GOLOVATCH (1992) a décrit une nouvelle espèce qu'il a attribuée au genre *Cutervodesmus* Kraus, 1957 et qui semble présenter sur les P.2 une conformation similaire à celle que nous avons trouvée chez *Venezuelodesmus*. Cependant, notre collègue GOLOVATCH ne dit rien du long organe qui s'évagine entre les segments 2 et 3. En outre, les trois espèces du genre *Venezuelodesmus* n. g. diffèrent de l'espèce décrite du Brésil par trois caractères :

1) les mandibules prolongées par une grande lamelle crénelée,
2) des processus sur la partie ventrale du 5ème segment,
3) la présence d'une branche séminale sur les gonopodes.

Considérant l'ensemble des genres réunis dans la famille des Fuhrmannodesmidae (BRÖLEMANN, 1916), il nous semble que cette immense famille, apparemment hétérogène, est mal définie et probablement polyphylétique. En tout cas, une révision de ces genres paraît nécessaire ainsi que la description de nouveaux taxons, qui mèneront sans doute à une nouvelle définition des sous-familles et des tribus.

Tenant compte des remarquables caractères du nouveau genre, *Venezuelodesmus* n. g., nous proposons pour celui-ci une tribu à part, la tribu Venezuelodesmini nov. trib.

RÉFÉRENCES

ATTEMS, C. , 1926. — Myriopoda. *In* : W. KÜKENTHAL & T. KRUMBACH, *Handbuch der Zoologie*, **4**, *Progoneata, Chilopoda, Insecta*, Berlin & Leipzig, W. de Gruyter & C° : 1-402.

ATTEMS, C., 1940. — Myriapoda 3. Polydesmoidea III. *In* : F. E. SCHULZE, W. KÜKENTHAL & K. HEIDER, *Das Tierreich*, **70**, Berlin & Leipzig, W. de Gruyter & C° : 1-577.

Source : MNHN, Paris

BRÖLEMANN, H. W., 1916. — Essai de classification des Polydesmiens (Myriapodes). *Ann. Soc. Entom. France*, **84** : 523-608.

DECU, V., BORDON, C. & LINARES O., 1987. — Las estaciones de América del Sur de donde ha sido colectado el material zoologico que esta en presente en estudio en el Instituto de Espeleologia de Bucarest (Romania). Situacion del material. *In : Fauna hipogea y hemiedafica de Venezuela y otros paises de América del Sur. 1.* Bucuresti, Ed. Acad. : 29-45.

GOLOVATCH, S. I., 1986. — Diplopoda from the Nepal Himalayas: Polydesmidae, Fuhrmannnodesmidae. *Senckenbergiana biol.*, **66** : 345-369.

GOLOVATCH, S. I., 1992. — Review of the Neotropical fauna of the millipede family Fuhrmannodesmidae, with the description of four new species from near Manaus, Central Amazonia, Brazil (Diplopoda, Polydesmida). *Amazoniana, Kiel*, **12** : 207-226.

HOFFMAN, R. L., 1980. — *Classification of the Diplopoda.* Genève, Muséum d'Histoire Naturelle, (1979), 237 pp.

JEEKEL, C. A. W., 1965. — The identity of *Dalodesmus tectus* Cook, 1896, and the status of the family names Dalodesmidae Cook, 1896, Vanhoeffeniidae Attems, 1914 and Sphaerotrichopodidae Attems, 1914 (Diplopoda, Polydesmida). *Entom. Bericht.*, **25** : 236-239.

KRAUS, O., 1957. — Myriapoden aus Peru, V. *Senck. biol.*, **38** : 95-114.

KRAUS, O., 1959. — Myriapoden aus Peru, VII. *Senck. biol.*, **40** : 191-208.

KRAUS, O., 1960. — Myriapoden aus Peru, IX. *Senck. biol.*, **41** : 241-264.

LOOMIS, H. F., 1964. — The Millipeds of Panama (Diplopoda). *Fieldiana Zoology*, **47** : 1-136.

MAURIÈS, J. P., 1983. — Le genre *Galliocookia* Ribaut, 1954. Deux espèces nouvelles des grottes de l'Ardèche et du Gard (Myriapoda, Diplopoda, Polydesmida). *Bull. Soc. Hist. nat., Toulouse*, **119** : 103-110.

SHEAR, W. A., 1973. — Millipeds (Diplopoda) from Mexican and Guatemalan caves. *Subterranean Fauna of Mexico, Acad. Nazionale Lincei*, **171** : 239-305.

SIMONSEN, A., 1990. — *Phylogeny and biogeography of the Millipede Order Polydesmida, with special emphasis on the Suborder Polydesmidea.* Thesis, Bergen, Mus. Zool. Univ., 114 pp.

TABACARU, I., 1975. — *Napocodesmus florentzae* n. sp. (Diplopoda, Polydesmida). *Trav. Inst. Spéol. E. Racovitza*, **14** : 71-82.

TABACARU, I., 1980. — *Trichopolydesmus (Banatodesmus) jeanneli* n. sg., n. sp. (Diplopoda, Polydesmida). *Trav. Inst. Spéol. E. Racovitza*, **19** : 155-161.

VANDEL, A., 1943. — Essai sur l'origine, l'évolution et la classification des Oniscoidea (Isopodes terrestres). *Bull. biol. Fr. Belg.*, **Suppl. 30** : 1-136.

VERHOEFF, K. W., 1910. — 4. Über Diplopoden 42. Aufsatz : Neue Polydesmiden aus Mitteleuropa und ihre Verwandten. *Zool. Anz.*, **36** : 132-145.

VERHOEFF, K. W., 1926-1932. — Diplopoda 1 & 2. *In* : H. G. BRONNS *Klassen und Ordnungen des Tierreichs*, **5**, Leipzig, Akademische Verlagsgesellschaft : 1-2084.

VERHOEFF, K. W., 1941. — Höhlen-Diplopoden aus dem Trentino. *Zeits. f. Karst. u. Höhlen.* : 179-189.

VERHOEFF, K. W., 1942. — Chilopoden und Diplopoden. *In* : *Beiträge zur Fauna Perus I*, Hamburg : 5-72.

Source : MNHN, Paris

Records of Paradoxosomatid Millipedes of India

***Kubra* BANO**

Department of Zoology, University of Agricultural Sciences, G.K.V.K., Bangalore, 560065, India.

ABSTRACT

A review of the family Paradoxosomatidae along with a list of genera and species so far recorded from India has been brought in this short paper.

RÉSUMÉ

Ce travail présente une revue taxinomique de la famille Paradoxosomatidae, accompagnée d'une liste des genres et espèces actuellement répertoriés en Inde.

INTRODUCTION

The family Paradoxosomatidae was first proposed by DADAY (1889) for the two genera of the order Polydesmida, *Trachydesmus* and *Paradoxosoma.* COOK (1895) recognized the family Paradoxosomatidae. In addition, he created a family Strongylosomatidae, a heterogenous group that was later considered synonymous to Paradoxosomatidae (JEEKEL, 1968).

ATTEMS (1898), in his monograph of the order Polydesmida, rejected the name Paradoxosomatidae, but recognized the family Polydesmidae in which he included the sub-family Strongylosominae, which included a number of genera along with *Trachydesmus* and *Paradoxosoma.* Apart from this, he distinguished the sub-family Suliciferinae. Both the sub-families were quite heterogenous as are almost all of the genera that are now included and referred to as Paradoxosomatidae. Subsequently, ATTEMS (1914), in his revised studies, merged these two sub-families into a single family Strongylosomidae. He published his work as a monograph in 1937 "*Das Tierreich*" vol. 68. His work included a description of the genera and species known up to 1937. This book acquired importance among the workers and became the origin for all the subsequent studies on the order. Following this, a number of contributions were made towards the revision, criticism and re-classification of the family Paradoxosomatidae (HOFFMAN, 1953, 1961, 1963, 1964; JEEKEL, 1963 a, b).

HOFFMAN critically evaluated the classification of Ethiopian fauna and briefly reviewed the genera. He also commented on the fauna of East Asia (HOFFMAN, 1961, 1963). JEEKEL (1963) presented a survey of the Paradoxosomatidae of the Neo-tropical regions and his publications dealt with the taxonomy of the Indo-Australian fauna. Further, he set right the anomaly in the classification to a certain extent arranging the so far known genera and species of Paradoxosomatidae according to their zoo-geographic regions (JEEKEL, 1968). He discussed

BANO, K., 1996. — Records of paradoxosomatid millipedes of India. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 73-77. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

and evaluated previously proposed classifications, bringing numerous changes in the generic delimitation of the fauna of several regions, including India.

ATTEMS (1937) estimated about 490 species of millipedes of the family Paradoxosomatidae whereas, in 1968, JEEKEL estimated 650 species. However, how many more might have gone unsighted and remained obscure is not known. JEEKEL (1963a) stated that "to the family Paradoxosomatidae are referable all genera included in the monograph on the Strongylosomidae published by ATTEMS, 1937, with the exception of *Aphelidesmus* Brol., *Iulidesmus* Silv., *Antisoma* Chamb., *Fijiodesmus* Chamb., *Phyletodesmus* Chamb., *Semenellogon* Chamb. and *Strongylomorpha* Silv.". In the same paper JEEKEL reinstated the name Paradoxosomatidae which, up to that time was mostly referred as Strongylosomidae or Strongylosomatidae.

According to the present state of our knowledge, the family is the largest of the order Polydesmida, which in turn is the largest order of the class Diplopoda.

The main character used for distinguishing Paradoxosomatidae is the presence of unconnected gonopod coxae, which are not joined by membranous bridge as in the other Polydesmid families. Coupled with this are the other typical features namely the unique presence of a distinct post-femoral cingulum in the gonopods, mode of insertion of the coxal horn in the gonopod coxa and the location of paired setae on the paraprocts.

Owing to the scantiness of the Indian faunistic studies, much remains to be done in the way of revisionary studies of the described species. ATTEMS (1936) was the first to study and describe some of the species belonging to this family under the name Strongylosomidae. Some notes have been furnished concerning *Anoplodesmus* (JEEKEL, 1965), *Chondromorpha* (JEEKEL, 1963a) and *Sundanina* (JEEKEL, 1953), but information on many genera is still lacking. To strengthen the studies, the author has carried out this review work and has planned to conduct a survey and studies on the family Paradoxosomatidae.

JEEKEL (1968) presented the diversity and distribution of oriental fauna and published a consolidated list of the fauna known till then, from which a list of the Indian paradoxosomatids has been brought out here, for the reference of the Indian workers. The list includes millipedes belonging to the four tribes, namely Sulciferini, Xanthodesmini, Sundanini and Polydrepanini. Of the four, the first three belong to the sub-family Paradoxosomatinae and the fourth to Alogolykinae.

CHECK-LIST OF PARADOXOSOMATID MILLIPEDES OF INDIA

List of species recorded by ATTEMS (1937) and reported by JEEKEL (1968)

1. *Orthomorpha (Kalorthomorpha) coonoorensis* Carl, 1932
2. *O. (K). ursula* Attems,1932
3. *O. (K). dentata* Carl, 1932
4. *O. (K). almorensis* Turk, 1947
5. *Anoplodesmus tanjoricus* (Pocock, 1892)
6. *A. anthracinus* Pocock, 1895
   (Syn. *Jonespeltis splendidus* Verhoeff, 1936)
7. *A. insignis* Attems, 1936
8. *A. saussurii* (Humbert, 1865)
9. *A. indus* (Chamberlin, 1920)
10. *A. atopus* (Chamberlin, 1920)
11. *Chondromorpha severini* Silvestri, 1897
12. *C. severini* var. *robusti* Attems, 1936
13. *C. mammifera* Attems, 1936
14. *C. kelaarti* (Humbert, 1865)
15. *C. kelaarti* sub. sp. *valparaiensis* (Carl, 1932)

Source : MNHN, Paris

16. *C. kelaarti* sub. sp. *longipes* (Verhoeff, 1936)
17. *C. kaimura* Turk, 1947
18. *Paranedyopus subcylindricus* Carl, 1932
19. *Himantogonus rufocinctus* (Carl, 1932) Comb. nov.
20. *Streptogonopus phipsoni* (Pocock, 1892)
(Syn. *Strongylosoma contortipes* (Attems, 1898)
21. *S. nitens* Attems, 1936
22. *S. jerdani* (Pocock, 1892)
23. *Sundanina nulla* Attems, 1936
24. *S. laevisulcata* Carl, 1932
25. *S. hirta* Carl, 1932
26. *S. contortipes* (Schubart, 1935)
27. *S. granulifera* Attems, 1936
28. *S. bimontana* Carl, 1932
29. *S. trifida* Carl, 1941
30. *S. pumila* Attems, 1944
31. *S. septentrionalis* Turk, 1947
32. *Dasypharkis rugulosa* (Carl, 1932)
33. *Polydrepanum tamilum* Carl, 1932
34. *P. implicatum* Carl, 1941
35. *Telodrepanum badaga* Carl, 1932
36. *Grammorhabdus asperrimum* Carl, 1932
37. *Xiphidiogonus spinipleurus* Carl, 1932
38. *X. dravidus* Carl, 1932
39. *X. hendersoni* Carl, 1932
40. *Gyrodrepanum contortipes* (Carl, 1932) Comb. nov.
41. *Kaschmiriosoma contortipes* (Schubart, 1935)

From the above list JEEKEL, in the same work, pointed out that the "*Orthomorpha*"*coonoorensis*, "*O*". *almorensis*, "*O*". *dendata*, "*Polydrepanum*" *implicatum*, "*Sundanina*" *granulifera*, "*S*". *trifida*, "*S*". *hirta*, "*S*". *simplex* and "*S*". *septentrionalis* belonged to unnamed genera, and stated that the allocation to definite genera could be done only after a careful study of the pertinent material.

JEEKEL (1980) reexamined some of the Indian species of paradoxosomatids and proposed two new genera, *Parchondromorpha* and *Harpagomorpha* of the tribe Suliciferini for the species *Orthomorpha coonoorensis* (Carl, 1932) and *Orthomorpha dentata* (Carl, 1932) respectively. He erected a nov. gen. for *Sundanina laevisulcata* (Carl, 1932) and *Sundanina hirta* (Carl, 1932): the genus *Antichirogonus*. In the same work, he described the characteristics of the genera *Polydrepanum* Carl, 1932 and *Dasypharkis* Attems, 1936 of the tribe Polydrepanini. He discussed the status of the tribes Polydrepanini and Alogolykini. He also reported *Desmoxytes planata* Pocock from the Andamans.

The following are the Indian paradoxosomatids reported by JEEKEL (1980):

1. *Paranedyopus rufocinctus* (Carl, 1932)
2. *Paranedyopus subcylindricus* (Carl, 1932)
3. *Paranedyopus simplex* (Humbert, 1865) new comb.
4. *Paranedyopus ursula* (Attems, 1936) new comb.
5. *Parchondromorpha coonoorensis* (Carl, 1932)
6. *Harpagomorpha dentata* (Carl, 1932)
7. *Antichirogonus laevisulcatus* (Carl, 1932)
8. *Antichirogonus hirtus* (Carl, 1932)
9. "*Kronopolites*" *unicolor* Attems, 1936
10. "*Kronopolites*" *spiniger* Attems, 1936
11. "*Strongylosoma*" *montigena* Carl, 1935
12. *Dasypharkis* Attems, 1936 (2 sp.)

Source : MNHN, Paris

13. *Gyrodrepanum* Carl, 1932 (1 sp.)
14. *Polydrepanum* Carl, 1932 (2 sp.)
(Syn. *Grammorhabdus* Carl, 1932)
15. *Telodrepanum* Carl, 1932 (1 sp.)
16. *Xiphidiogonus* Carl, 1932 (3 sp.)
17. *"Polydrepanum" implicatum* Carl, 1941
18. *"Sundanina" granulifera* Attems, 1936
19. *"Sundanina" trifida* Carl, 1941
20. *Desmoxytes planata* (Pocock, 1895)
(Syn. *Prionopeltis planatus* Pocock, 1895)

JEEKEL listed the genera that are under inverted commas above, as *incertae sedis* and stated that these required reexamination of the gonopods for proper allocation to their genera.

GOLOVATCH (1984) examined the millipedes collected from India by Dr. G. TOPAL of the Hungarian Natural History Museum, Budapest, in 1967, and discovered some very important specimens of paradoxosomatids. He distinguished 16 species belonging to 13 genera of this family. Among these, 9 were found to be new to science. He erected 8 new genera and synonymised one. His work presented the description and allocation of the new taxa established by him.

The following is the list of paradoxosomatids which Dr. GOLOVATCH listed from the collection of Dr G. TOPAL.

A List of paradoxosomatid millipedes of India
(Reported by S. I. GOLOVATCH, 1983, 1984)

1. *Kaschmiriosoma contortipes* Schubart, 1935
2. *Chondromorpha mammifera* Attems, 1936
3. *Kronopeltis occidentalis* Golovatch, 1983
4. *Topalosoma setiferum* sp. nov. Golovatch, 1984
5. *Curiosoma bispinosum* sp. nov. Golovatch, 1984
6. *Polydrepanum horridum* sp. nov. Golovatch, 1984
7. *Hindomorpha (=Sundanina) granulifera* (Attems, 1936)
8. *Parchondromorpha indica* sp. nov. Golovatch, 1984
9. *Parchondromorpha similis* sp. nov. Golovatch, 1984
10. *Armolites spiniger* (Attems, 1936)
11. *Laterogonopus simplex* sp. nov. Golovatch, 1984
12. *Substrongylosoma distinctum* sp. nov. Golovatch, 1984
13. *Substrongylosoma falcatum* sp. nov. Golovatch, 1984
14. *Himalomorpha montigena* (Carl, 1935)
15. *Paranedyopus cylindricus* comb. nov. (Carl, 1935)
16. *Paranedyopus elongissimus* sp. nov. Golovatch, 1984

The above lists constitute a record of the Indian paradoxosomatid millipedes reported so far.

ACKNOWLEDGEMENTS

The author thanks Dr. C. A. W. JEEKEL, Amsterdam, Netherlands and Dr. S. I. GOLOVATCH of the Institute of Evolutionary Morphology and Ecology of Animals, Russian Academy of Sciences, Moscow, for their help in providing the literature on Paradoxosomatidae. She also thanks Dr. J.-J. GEOFFROY of M.N.H.N., Paris for his help in the presentation of the results during the 9th International Congress of Myriapodology, Paris, France, July 1993.

REFERENCES

ATTEMS, C., 1898. — System der Polydesmiden 1. Teil. *Denkschr. K. Akad. Wiss. Wien (Math. Naturwiss cl.)*, **LXXVII** : 221-482.

ATTEMS, C., 1914. — Die Indo-Australischen Myriopoden. *Arch. Nat. Abt. AH*, **80** : 1-398.

Source : MNHN, Paris

ATTEMS, C., 1936. — Diplopoda of India. *Mem. Ind. Mus.*, **11**.

ATTEMS, C., 1937. — Myriapoda 3. Polydesmoidea. I. Fam. Strongylosomidae. *In* : F. E. SCHULZE, W. KÜKENTHAL & K. HEIDER, *Das Tierreich*, **68**, Berlin & Leipzig, W. de Gruyter & C° : 1-300.

COOK, O. F., 1895. — Introductory note on the families of Diplopoda. *In*: : O. F. COOK & G. N. COLLINS, *The Craspedosomatidae of North America. Ann. New-York Acad. Sci.*, **9** : 1-8.

DADAY, E., 1889. — Myriopodie estranea Musaei nationalis Hungarici. *Termèszetr. Füz.*, **12** : 115-156.

GOLOVATCH, S. I., 1983. — Two Paradoxosomatidae from the Kashmir, Himalayas (Diplopoda). *Senckenberg. Biol.*, **63** : 297-302.

GOLOVATCH, S. I., 1984. — Some new or less known Paradoxosomatidae (Diplopoda: Polydesmida) from India. *Acta Zoologica Hungarica* , **30** : 327-352.

HOFFMAN, R. L., 1953. — *Scolodesmus* and related African millipede genera (Polydesmida : Strongylosomatidae). *Proc. Biol. Soc. Wash.*, **66** : 75-84.

HOFFMAN, R. L., 1961. — Two new Diplopod genera from Western China (Polydesmida : Strongylosomatidae). *Ann. Mag. Nat. Hist.*, **13** : 533-543.

HOFFMAN, R. L., 1963. — A contribution to the knowledge of Asiatic Strongylosomoid Diplopoda (Polydesmida: Strongylosomatidae). *Ann. Mag. Nat. Hist.*, **13** : 577-593.

HOFFMAN, R. L., 1964. — Über einege Ostafrikanishe Diplopoda Polydesmida der zoologischen Statsammlung München. *Opusc. Zool. München.*, **79** : 1-10.

JEEKEL, C. A. W., 1953. — Two new Strongylosomidae from Indochina (Diplopoda, Polydesmidae). *Beaufortia*, **2** : 1-8.

JEEKEL, C. A. W., 1963a. — Diplopoda of (1-5) slud. *Fauna Surinam* , **4** : 1-157.

JEEKEL, C. A. W., 1963b. — Paradoxosomatidae from Borneo (Diplopoda: Polydesmida). *Tijdschr. Ent.*, **106** : 205-283.

JEEKEL, C. A. W., 1965. — A revision of the Burmese Paradoxosomatidae (Diplopoda, Polydesmida) in the Museo Civico di Storia Naturale at Genova (Part I). *Tijdschr. Ent.*, **108** : 95-144.

JEEKEL, C. A. W., 1968. — *On the classification and geographical distribution of the family Paradoxosomatidae (Diplopoda - Polydesmida)*. Amsterdam, 162 pp.

JEEKEL, C. A. W., 1980. — On some little known Paradoxosomatidae from India and Ceylon, with the description of four new genera (Diplopoda: Polydesmida). *Beaufortia*, **30** : 163-178.

Source : MNHN, Paris

Source : MNHN, Paris

Systematics and Biogeography of *Ctenophilus* Cook, 1898. A Genus of Centipedes with Disjunct Distribution (Geophilomorpha, Schendylidae)

Luis A. PEREIRA

Museo de La Plata, Paseo del Bosque s/n, 1900-La Plata, Argentina

ABSTRACT

Among all known genera of Schendylidae *Ctenophilus* Cook, 1898 is the only one characterized by having the pleurites of the second maxillae fused with the posterior border of the coxosternum (apomorphic state of the character). In all the remaining genera of the family the pleurites are not fused (plesiomorphic state of the character).

This genus has a wide distribution in Africa, with twelve species known to date. It is also present (but much less widespread) in the Neotropical Region with one species in the Caribbean area.

A historical summary is provided for the genus, as well as observations on the taxonomic significance of various characters heretofore utilized to distinguish genera of Schendylids.

Ctenophilus amieti (Demange, 1963), *C. chevalieri* (Brölemann & Ribaut, 1911), *C. corticeus* (Demange, 1968), *C. edentulus* (Porat, 1894), *C. magnus* (Demange, 1963), *C. nesiotes* (Chamberlin, 1918), *C. nitidus* (Brölemann, 1926), *C. oligopodus* (Demange, 1963) and *C. pratensis* (Demange, 1963) are redescribed and figured from type material and/or additional specimens and a map showing the geographical distribution of all species of the genus is included.

It is not known enough about the genus *Ctenophilus* and its nearest relatives to be able to confidently suggest an explanation of the amphiatlantic pattern of distribution (which is common to some other genera of geophilomorphs such as *Schendylurus*, *Pectiniunguis*, etc.). Plate tectonic events are considered being very evident the convinience to develop a cladistical analysis within the Schendylids together with a biogeographical study.

It is also considered the case of the halophilous geophilomorphs. The scattered and often wide-ranging distribution of these centipedes has been commented upon several times, specially by CLOUDSLEY-THOMPSON (1948), CRABILL (1960) and KEVAN (1983). Such species are very probably dispersed by rafting across very large distances, although in a very impredictable way. CRABILL (1960) even suggested that this way of dispersal might explain trans-Atlantic disjunction between South America and Africa. More data are obviously required and individual cases must be investigated in depth before we can assess the actual extent of this phenomenon and its possible occurence within *Ctenophilus*.

RÉSUMÉ

Systématique et biogéographie de *Ctenophilus* Cook, 1898 ; un genre de chilopodes à aire disjointe (Geophilomorpha, Schendylidae).

Ce travail propose une révision de l'ensemble du genre *Ctenophilus* Cook, largement répandu d'une part en Afrique (12 espèces), d'autre part dans la zone néotropicale (1 espèce dans l'aire Caraïbe). La révision de la systématique et de la classification des espèces composant le genre conduit à une discussion relative aux modalités de sa dispersion en deux aires actuellement disjointes et éloignées.

PEREIRA, L. A., 1996. — Systematics and biogeography of *Ctenophilus* Cook, 1898. A genus of centipedes with disjunct distribution (Geophilomorpha, Schendylidae). *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 79. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

Source : MNHN, Paris

Review and Perspective of Study on Myriapodology of China

*Daqing*WANG * & *Jean-Paul* MAURIÈS **

* Department of Invertebrates, Institute of Zoology
Chinese Academy of Sciences, Beijing 100080
** Muséum National d'Histoire Naturelle, Laboratoire de Zoologie/Arthropodes
61, rue Buffon, F-75231 Paris, France

ABSTRACT

This contribution reviews the history and the present state of research in Myriapodology in China. It introduces all Chinese researchers and their work in the field. Considering the present state of knowledge of Myriapoda, perspectives and some suggestions are presented for future studies in this field in China.

RÉSUMÉ

Bilan et perspectives des recherches myriapodologiques en Chine.

Ce travail passe en revue le développement historique et l'état actuel des recherches myriapodologiques en Chine. Il fait état des travaux de tous les chercheurs chinois dans ce domaine. Un certain nombre de perspectives sont dégagées et des suggestions sont proposées en vue de futurs travaux sur ce sujet en Chine.

INTRODUCTION

The features of Chinese zoogeography and geology are unusual and diverse. Zoogeographically, China covers two zones: the orient and the palearctic. Physiographically, China occupies 6.5% of the land surface of the world. The varied features make China abundant in diversity of animal species. However, the present situation of study on Myriapoda of China does not match in possibility provided by the fauna.

The starting point of the modern period of myriapology in China began in the late 1940s, when the study of Taiwan diplopods commences. Studies on the Chinese mainland only began in the late 1970s, since when a relatively prosperous period of myriapod study started. For many years, only a small fraction of the actual China myriapod fauna and the work of Chinese myriapodologists were known. An important reason for this is the language barrier because many papers published by Chinese scientists were only accompanied by a brief abstract in English. Hence the present paper is intented to introduce the current situation of Chinese myriapodology in five sections: historical review and perspective, literature survey, collecting localities, checklist of taxa, geographical and physiographical notes.

WANG, D. & MAURIÈS, J.-P., 1996. — Review and perspective of study on myriapodology of China. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 81-99. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

GEOGRAPHICAL, PHYSIOGRAPHICAL AND GEOLOGICAL NOTES

The present nation of China occupies an area of about 9.6 millions km2, of which lies on the east of Euro-asian continent and the western coast of the Pacific Ocean. China has an ancient and complex geology. In terms of Plate Tectonics, China basically belongs to the Eurasian-plate, connecting with the Indo-plate in south and jointing the Pacific-plate of the Philippine-plate in the East. The geological history of China is the result of the interactions of the three plates mentioned above.

The Sino-Indo orogenic movement was the key factor in the formation of the Chinese region in the early Mesozoic. From that time, the outline of the region was fundamentally formed. From Yianshan orogenic movement to the early Tertiary, the land surface of China and the rest of the world has been relatively stable. The surface became lower and flatter because of chronic erosion and weathering, and the climate became warmer.

The Himalayan orogenic movement was directly responsible for the formation of the modern physiographical environment of China during the Cenozoic. The great orogenic movement comprised two events: the first occured from the late Oligocene to the Middle Miocene; the second continued from the late Pliocene to the early Pleistocene, this being the more sporadic orogen.

The second orogenic event was the most significant factor in the formation of the modern physiographical variations of China. Under the force of the Himalayan orogenic movement, the physiographical environment of the Euro-asian continent greatly changed: the ancient Mediterranean sea disappeared; the Euro-asian continent jointed together; the great Tibetan plateau emerged and became the worlds crest. Due to these events, the climate of China consequently changed.

The elevation of the Tibet plateau, which blocked the moist winds from the ocean, resulted in the formation of an arid physiographical environment in western China. To a large extent, other regions succeeded the tropical or subtropical environment which formed before the Quaternary.

HISTORICAL REVIEW AND PERSPECTIVE

Myriapods have been collected and recorded in China for more than 2000 years because the Chinese use some species, notably centipedes, in medicine. According to traditional Chinese medicine, large centipedes, such *Scolopendra*, can treat diseases, such carbuncles, scabies and the sting of some insects. This is based on the traditional medicine theory that one poison can be overcome by another. Hence, for a long time, the collection and study of Chinese myriapods has focused on the medicinal use of centipedes, particularly large species. Up to now, people in countries of southern China have a habit that treat stings of insects by using the alcohol in which centipedes have been immersed.

The Chinese Encyclopedia of material medicine, named "Ben Cao Gang Mu", edited in 1596, listed this as a kind of animal medicine and described its medicinal effects in detail. As a result, some medical experts have analyzed centipede toxins using biochemical techniques. However, the scientific study of the systematics of Chinese myriapods did not start until this century.

The first such study dealing with Chinese myriapods dates from the late 1940s, when Professor WANG Youxie (Yu-Hsi) commenced the study of diplopods of Taiwan. This was the first time that Chinese myriapodologists had studied Chinese myriapods by themselves. In his early study career, WANG sent collections of millipedes and centipedes to LOHMANDER to identify. Later, much work was accomplished by himself towards the description and identification of specimens from Taiwan and it adjacent islands. Most of his papers were published in the *Quaterly Journal of the Taiwan Museum*. After the late 1960s his name

Source : MNHN, Paris

disappeared from the literature. One of us (W. D.) asked several entomologists from Taiwan about him, but to no avail. In 1950, the Chinese archaeologists JIA Lanpuo and LIU Xianting discovered several fossil myriapods in Choukoutien, Beijing, and their paper was published in the *Bulletin of the Geological Society of China*. This was the first time that the fossil myriapods were reported in China.

Since the 1970s, Professor ZHANG Chong-Zhou has begun the systematic study of mainland Chinese myriapods, including Diplopoda, Chilopoda, Symphyla and Pauropoda. From that time, myriapodology was just known in China as a systematics owing to Professor ZHANG's outstanding work.

From 1976 to 1979, Professor ZHANG was mainly engaged in the studies of medicinal centipedes, including their ecological habitats, individual development and breeding. In 1977, ZHANG reported a new species of spirostreptoid collected by LI Zhi-Yin from Yunnan. In 1978, he described myriapods collected by the same collector from Xisha islands. In 1980, he reported a preliminary study on the Symphyla of China, based on material collected by CHEN Zhong-Pin from Jinhua, Zhejiang.

From 1981 to 1983, ZHANG & LI described five new species belonging to five different groups of millipedes, described the new family Bilingulidae in 1981, and redescribed *Scolopendra mazbii*, collected by LI Zhi-Yin from Tibet, in 1983. The next year, ZHANG Chong-Zhou published a new xystodesmoid, taken by MAO Jerong from Zhejiang province and, in the same year, LI Zhi-Yin published a summary of centipede species of medicinal use. From 1985 to 1990, ZHANG Chong-Zhou reported three new species taken by LI from southwestern China, and described a new genus and species of harpagophoroid collected by ZHANG Nai-Gang from Yunnan in 1990.

In 1988 an important paper by ZHANG & CHEN Zhong-Pin appeared on Pauropoda from Zhemiang province, listing eight species, four of which were described as new. This paper also gave the first checklist of Pauropods in China. CHEN Jian-Xiu & MENG Weng-Xin described a new cambalopsoid in 1991, but have not published since. In 1992, ZHANG & WANG Daqing reported six subtropical soil species in a resource survey on centipedes for medicinal use from Wuling mountain. In 1993, WANG Daqinq reported six species of diplopods, three of them as new, based on material from Fujian province.

By the end of 1993, more than 300 species taxa of myriapods had been described or reported from China in the papers listed in the references. Obviously, we probably know only 5% of the actual and real number of taxa that occur in China, perhaps even less...

PERSPECTIVES AND SUGGESTIONS

From the summary given above, we may get two kinds of impressions: one is that there are only a few researchers who are engaged in the study of myriapods in China; the other is that the research mainly focuses on the description of new species, and lacks systematic and in-depth studies. One of the reasons for this is that the study of myriapodology in China started late. Another reason is the large size of China. Finally the study of myriapodology currently belongs to the range of basic science, so that research funds are difficult to obtain, because the result of study cannot quickly bring profit, especially in the reality of China today. Perhaps the latter is the reason why few young specialists are interested in this field. Although this situation results in a vicious circle, it does not necessarily mean that systematics will disappear. On the contrary, we believe that systematics will prospere again, with the appearance of cladistics as an example. And we believe that this could be soon, because there are, after all, many old and young researchers willingly engaged in the study of myriapodology. However, it is true that we face a very serious challenge, especially in China.

In order to overcome such a situation in China, perhaps it might be practicable to systematically study other uses for medicinal myriapods, as food for instance (centipedes can be)

Source : MNHN, Paris

or by extracting the pure toxin from their bodies to treat disease in order to obtain money for less applied studies. If successfull, it would be a beneficial circle.

China is a large region including two zoogeographical zones. The study of Chinese myriapodology needs a large number of biological researchers to join in, including foreign myriapodologists. Therefore, it is important to develop all kinds international co-operation and communication. The study of Chinese myriapod fauna will contribute to the myriapod fauna of the world.

At present in China, the systematic and detailed study of some taxa such as the orders Julida, Polydesmida and Scolopendromorpha, should carried out first. The next stage would be to cover these orders in the two zoogeographical zones. The third will be devoted the study of zoogeography in the two zones. These are just suggestions. It is earnestly hoped that this paper will provide a usefull appeal to present and future researchers of Chinese Myriapoda, who will be able to join us and to build their own greater and finer edifices.

PROVISIONAL CHECKLIST OF MYRIAPOD SPECIES OF CHINA

The following preliminary list is mainly compiled from the papers published in China, the partial from abroad. Because the literature is so scattered and many are new reports, especially some published in Chinese, authors and dates of publications for species have been included.

Class DIPLOPODA

Subclass Penicillata
- Order Polyxenida
  - Fam. Polyxenidae
    - *Polyxenus hangzoensis* Ishii & Liang, 1990
    - *Eudigraphis taiwaniensis* Ishii, 1990
    - *Eudigraphis sinensis* Ishii & Liang, 1990
  - Fam. Lophoproctidae
    - *Lophoturus okinawai* (Nguyen Duy - Jacquemin & Condé, 1982) - Ishii, 1990

Subclass Pentazonia
- Order Sphaerotheria
  - Fam. Sphaeropoeidae
    - *Chinosphaera majorina* Zhang & Li, 1982
    - *Chinosphaera maculosa* Attems, 1935
    - *Chinosphaera multidenta* Wang & Zhang, 1993
    - *Zephronia (?) profuga* Attems, 1936
    - *Zephronia (?) hainana* Gressitt, 1941
- Order Glomerida
  - Fam. Glomeridae
    - *Hyleoglomeris sinensis* (Brölemann, 1896)
    - *Hyleoglomeris emarginata* Golovatch, 1981
- Pentazonia incertae sedis
    - "*Glomeris*" *bicolor* (Wood, 1865)

Subclass Colobognatha
- Order Platydesmida
  - Fam. Andrognathidae
    - *Sinocybe cooki* Loomis, 1942
    - *Symphyopleurium hozawai* (Chamb. & Wang, 1953)
- Order Siphonophorida
  - Fam. Siphonophoridae
    - *Siphonophora* sp. (Wang, unpublished)

Subclass Helminthomorpha
- Supraorder Iuliformia
  - Order Fossil
    - "*Iulus*" *peii* Chioa & Liu, 1951: 24
  - Order Spirobolida
    - Fam. Spirobolidae
      - *Spirobolus bungii* Brandt, 1833
        - = *Spirobolus exquisitus* Karsch, 1881

Source : MNHN, Paris

= *Spirobolus joannesi* Brölemann, 1896 - Wang, 1955, 1958
Spirobolus walkeri Pocock, 1895
Spirobolus cincinnalis Wang & Zhang, 1993
Spirobolus grahami Keeton, 1960
Spirobolus formosae Keeton, 1960
Spirobolus umbobrochus Keeton, 1960
Trigoniulus niger Takakuwa,1940 - Wang, 1955
Trigoniulus takahasii Takakuwa, 1940
Trigoniulus segmentatus Takakuwa, 1940 - Wang, 1955, 1964
Trigoniulus tertius Takakuwa, 1940 - Wang, 1958
Spirostrophus lanyusis Wang, 1955
Spirobolellus tatakuwai Wang, 1961

Order Spirostreptida

Fam. Harpagophoridae

Gonoplectus astutus Attems, 1936
Junceustreptus retrorsus Hoffman, 1980
Junceustreptus browningi Demange, 1961
Junceustreptus prominulus Demange, 1961
Junceustreptus brevispinus Zhang, 1985
Uriunceustreptus afemorispinus Zhang & Chang, 1990
Agariogonopus acrotrifoliatus Zhang (in press)

Order Cambalida

Fam. Pericambalidae

Bilingulus sinicus Zhang & Li, 1981
Parabilingulus aramulus Zhang & Li, 1981

Fam. Cambalidae

Glyphiulus anophthalmus (Loksa, 1960)
Glyphiulus balaszi (Loksa, 1960)
Glyphiulus granulatus Gervais, 1847
= ? *Glyphiulus vulgatus* Zhang & Li, 1982
= ? *Glyphiulus tuberculatus* (Verhoeff, 1936) - Chamberlin & Wang, 1953, Wang, 1955, 1957
Glyphiulus formosa (Pocock, 1895)
Glyphiulus pulcher (Loksa, 1960)
Glyphiulus recticullus Zhang & Li, 1982
Glyphiulus multicarinus Zhang & Li, 1982
Glyphiulus adeloglyphus Zhang & Li, 1982
Glyphiulus quadrohamatus Chen & Meng, 1991

Order Julida

Fam. Nemasomatidae

Orinisobates gracilis (Verhoeff, 1933) - Enghoff, 1985
Sinostemmiulus simplicior Chamberlin &Wang, 1953 - Hoffman, 1966

Fam. Mongoliulidae

Skleroprotopus confucius Attems, 1901
Skleroprotopus laticoxalis Takakuwa, 1942
Skleroprotopus serratus Takakuwa & Takashima, 1949
Skleroprotopus membranipedalis Zhang, 1985

Fam. Paraiulidae

Karteroiulus niger Attems, 1909 - Enghoff, 1987

Fam. Julidae

Amblyiulus sp. Takakuwa & Takashima, 1949
Anaulaciulus paludicola (Pocock,1895) - Causey, 1966
Anaulaciulus simplex (Verhoeff, 1936) - Wang, 1964
Anaulaciulus tonginus (Karsch, 1881)
Anaulaciulus trapezoidus (Wang, 1955, 58, 63)
Anaulaciulus trilobus (Wang, 1963)
= *Anaulaciulus trilobus quemoyensis* (Wang, 1963)
Anaulaciulus trilobus khuuae (Wang, 1963)
Anaulaciulus vallicola (Pocock, 1895) - Causey, 1966
Nepalmatoiulus tibetanus Enghoff, 1987
Nepalmatoiulus rhaphimeritus Enghoff, 1987

Source : MNHN, Paris

Nepalmatoiulus brachymeritus Enghoff, 1987
Nepalmatoiulus polyakis Enghoff, 1987
Nepalmatoiulus fraterdraconis Enghoff, 1987
Nepalmatoiulus eulobos Enghoff, 1987
Nepalmatoiulus yunnanensis Enghoff, 1987

Supraorder Coelochaeta
Order Callipodida
Fam. Caspiopetalidae
Bollmania sp. Golovatch, 1981
Fam. Sinocallipodidae
Sinocallipus simplicipodus Zhang, 1993
Fam. Paracortinidae
Paracortina voluta Wang & Zhang, 1993
Paracortina leptoclada Wang & Zhang, 1993
Paracortina (Altum) carinata (Wang & Zhang, 1993)
Paracortina (Altum) serrata (Wang & Zhang, 1993)
Paracortina (Relictus) stimula (Wang & Zhang, 1993)
Paracortina (Relictus) thallina (Wang & Zhang, 1993)
Paracortina (Altum) viriosa (Wang & Zhang, 1993)
Order Craspedosomatida (=Chordeumatida auct.)
Fam. Diplomaragnidae
Syntelopodeuma gracilipes Verhoeff, 1941- Wang, 1958
Diplomaragna formosanum (Verhoeff, 1936) - Shear, 1990
Fam. Speophilosomatidae
Speophilosoma sp. Wang, 1958
incertae sedis
G.sp. Verhoeff, 1933 - Chamberlin & Wang, 1953

Superorder Merocheta
Order Polydesmida
Suborder Paradoxosomatidea
Fam. Paradoxosomatidae
Subfam. Alogolykinae)
Tribe Alogolykini
Yuennanina ceratogaster Attems, 1936
Yuennanina aceratogaster Zhang & Li, 1977
Yuennanina petalolobodes Chang & Zhang, 1989
Tribe Polydrepanini
Orophosoma hingstoni (Carl, 1935) - Jeekel, 1980
Orophosoma simulans (Carl, 1935) - Jeekel, 1980
Subfam. Paradoxosomatinae
Tribe Tectoporini
Helicorthomorpha holstii (Pocock, 1895) - Wang, 1955, Jeekel, 1980, Golovatch, 1981
= *Chinosoma hodites* Chamberlin, 1923
= *Kochliopus trivittatus* Verhoeff, 1933
Helicorthomorpha ocellata (Pocock, 1895) - Jeekel, 1980
= *Helicorthomorpha uncinata* (Attems, 1937)
Helicorthomorpha orthogona (Silvestri, 1898) - Jeekel, 1980
= *Helicorthomorpha kosingai* (Wang, 1958)
Tribe Sulciferini
Orthomorpha coarctata Saussure, 1860 - Wang, 1956, 1957
Oxidus gracilis C.L.Koch, 1847 - Pocock, 1895, Wang, 1955, Wang & Zhang, 1993
Hedinomorpha hummeli Verhoeff, 1933
Hedinomorpha hummeli svenhedini Verhoeff, 1933
Hedinomorpha biramipedicula Zhang & Tang, 1985
Kronopolites swinhoei (Pocock, 1895) - Hoffman, 1963
= *Kronopolites svenhedini* Verhoeff, 1933 - Zhang & Li, 1978
= *Kronopolites formosanus* (Verhoeff, 1939)
= *Kronopolites ralphi* Wang, 1957
Kronopolites acuminatus biagrilectus Hoffman, 1963

Source : MNHN, Paris

Mandarinopus gracilipes Verhoeff, 1933
Polylobosoma roseipes (Pocock, 1895) - Jeekel, 1980
= *Orthomorpha penicillata* Attems, 1931
Sichotanus mandschuricus Golovatch, 1978
Sigipinius grahami Hoffman, 1961
"*Orthomorpha*" (unnamed genus!) *nordenskjoeldi* Attems, 1909 - Wang, 1955, 1964
"*Orthomorpha*"(unnamed genus) *corticina* Attems,1936

Tribe Chamberlinini
Chamberlinius pekuensis (Karsch, 1881) - Wang, 1955 , Golovatch, 1981
= *Oxidus corcifera* Verhoeff, 1931 - Wang, 1957
= *Orthomorpha affinis* Verhoeff, 1936 - Takashima, 1939
Chamberlinius haulienensis Wang, 1956 - Hoffman, 1973
Chamberlinius shengmui Wang, 1957 - Hoffman, 1973
Chamberlinius picrofasciatus (Gressitt, 1941) - Hoffman, 1973

Tribe Hylomini
Desmoxytes planata (Pocock, 1895) = *D. rastrituberus* (Zhang, 1986)
Desmoxytes draco (Cook & Loomis, 1924)
Desmoxytes piceofasciata (Gressitt, 1941)
Desmoxytes longispina (Loksa, 1960)
Desmoxytes cornuta (Zhang & Li, 1982)
Desmoxytes minutubercula (Zhang, 1986)

Tribe Tonkinosomatini
Aponedyopus montanus Verhoeff, 1939 - Takakuwa, 1942 , Wang, 1964
Aponedyopus reesi (Wang, 1957)
Aponedyopus jeanae (Wang, 1957)
Aponedyopus maculatus Takakuwa, 1942
Szechuanella tenebra Hoffman, 1961

Tribe Nedyopodini :
Nedyopus patrioticus (Attems, 1898) - Wang, 1955, 1964
Varyomorpha hsientienensis Wang, 1957
Varyomorpha pectinata Wang, 1957

Paradoxosomatidae incertae sedis
Orthomorpha bisulcata Pocock, 1895 - Wang, 1957
Orthomorpha flavomarginata Gressitt, 1941
Gonebelus sinensis Attems, 1936
Strongylosoma nadari Brölemann, 1896
Orthomorpha endeusa Attems, 1898
Orthomorpha circularis Takakuwa in Takakuwa & Takashima, 1949

Suborder Polydesmidea
Superfam. Polydesmoidea
Fam. Polydesmidae
Polydesmus liber Golovatch, 1991
Pacidesmus sinensis (Golovatch & Hoffman, 1989) - Golovatch, 1991
= *Polydesmus hamatus* Loksa,1960
Epanerchodus potanini Golovatch, 1991
Epanerchodus shirinensis (Chamberlin & Wang, 1953)
Epanerchodus stylotarseus Chen & Zhang, 1990
Epanerchodus sphaerisetosus Zhang & Chen, 1983
Epanerchodus eurycornutus (Zhang, 1992)
Epanerchodus takakuwai Verhoeff, 1931 - Wang, 1958
Epanerchodus orientalis Attems, 1901 - Wang, 1956, 1964

Fam. Doratodesmidae
Eutrichodesmus arcicollaris Zhang & Wang, 1993
Crenatidorsus grandifoliatus Zhang & Wang, 1993
Pocillidorsus dorsiangulatus Zhang & Wang, 1993
Parapauroplus monodentus Zhang & Wang, 1993

Fam. Haplodesmidae
Prosopodesmus jacobsoni Silvestri, 1910, Wang, 1964

Fam. Cryptodesmidae
Niponia nodulosa Verhoeff, 1931 - Wang, 1955, 1964

Source : MNHN, Paris

Niponia simplexus (Wang, 1957)
Superfam. Stylodesmoidea
Fam. Pyrgodesmidae
Cryptocorypha spinicoronatus Zhang & Li, 1981
Delurodesmus orientalis Silvestri, 1948
Thelodesmus armatus Miyoshi, 1951 - Wang, 1958
Suborder Chelodesmidea
Superfam. Xystodesmoidea
Fam. Xystodesmidae
Tribe Orophini
Kiulinga jeekeli Hoffman, 1956
Kiulinga lobosa Zhang & Mao, 1984
Pamelaphe lacustris (Pocock, 1895) - Hoffman, 1964
Tribe Harpaphini
Riukiaria taiwanalis (Takakuwa, 1942)
Riukiaria uraensis (Wang, 1956)
Riukiaria holstii (Pocock, 1895) - Wang, 1964
Riukiaria neptuna (Pocock, 1895) - Wang, 1964
Riukiaria variata (Pocock, 1895) - Wang, 1964
Riukiaria capaca Wang & Zhang, 1993
Riukiaria ochraceus (Gressitt, 1941)
Riukiaria taiwanus (Takakuwa, 1942) - Chamberlin & Wang, 1953
Rhysodesmus (?) *cohaesivus* Wang, 1957
Rhysodesmus (?) *contiguus* Wang, 1957
Pachydesmus (?) *attemsi* Wang, 1960
Polydesmida incertae sedis
Polydesmus moorei Pocock, 1895
Polydesmus paludicola Pocock, 1895

Class CHILOPODA

Subclass Epimorpha
Order Geophilomorpha
Fam. Himantariidae
Stigmatogaster japonica Takakuwa, 1935
Fam. Schendylidae
Subfam. Schendylinae
Escaryus latzeli Sseliwanoff, 1881 - Attems, 1927
Escaryus japonicus Attems, 1927 - Takakuwa & Takashima, 1949, Wang, 1957
Escaryus sachalinus Takakuwa, 1935 - Takakuwa & Takashima, 1949
Subfam. Ballophilinae
Ballophilus liber Chamberlin, 1952
Thalthybius boteltoboensis Wang, 1955
Fam. Oryidae
Orphnaeus brevilabiatus Newport, 1845 - Pocock, 1895 , Wang, 1955
Fam. Geophilidae
Subfam. Geophilinae
Geophilus infossulatus Attems, 1901
Pleurogeophilus takakuwai Verhoeff, 1934
Subfam. Dignathodontinae
Paraplanes svenhedini Verhoeff, 1933
Scolioplanes transsilvanicum (Verhoeff, 1928) - Wang, 1959
Scolioplanes maritimus japonicus (Verhoeff, 1935) - Wang, 1959
Subfam. Pachymerinae
Pachymerium ferrugineum C.L. Koch, 1847 - Takakuwa, 1938, Wang, 1956, Takakuwa & Takashima, 1949
Pachymerium atticum Verhoeff, 1901 - Takakuwa & Takashima, 1949
Fam. Mecistocephalidae
Subfam. Mecistocephalinae
Formosocephalus longichilatus Takakuwa, 1937
Mecistocephalus rubriceps Wood, 1862 - Wang, 1956, 1959
Mecistocephalus mikado Attems, 1928 - Takakuwa, 1938, Wang, 1956

Source : MNHN, Paris

Mecistocephalus brevisternalis Takakuwa, 1934
Mecistocephalus fenestratus Verhoeff, 1934
Mecistocephalus takakuwai Verhoeff, 1934
Mecistocephalus ongi Takakuwa, 1934
Mecistocephalus multidentatus Takakuwa, 1936
Mecistocephalus japonicus Meinert, 1870 - Wang, 1963
Mecistocephalus nannocornis Chamberlin, 1920 - Wang, 1957
Mecistocephalus diversisternus Silvestri, 1919 - Wang, 1957
Mecistocephalus punctifrons Newport, 1845 - Wang, 1963
Mecistocephalus smithi Pocock, 1895 - Chamberlin & Wang, 1952 - Wang, 1955
Mecistocephalus mirandus Pocock, 1895
Mecistocephalus insularis (Lucas, 1863) - Attems, 1929, Wang, 1956, 1959
Mecistocephalus insulomontanus Gressitt, 1941
Mecistocephalus monticolens Chamberlin, 1920 - Wang, 1956
Nodocephalus dooi Takakuwa, 1940 - Wang, 1959
Nodocephalus edentulus Attems, 1910 - Wang, 1956, 1963
Nodocephalus pauroporus Takakuwa, 1936
Taiwanella striata Takakuwa in Takakuwa & Takashima, 1949
Taiwanella sculptulatus Takakuwa, 1936
Taiwanella yanagiharai Takakuwa, 1936
Tygarrup javanicus Attems, 1907 - Chamberlin & Wang, 1952

Subfam. Arrupinae

Prolamnonyx holstii (Pocock, 1895) - Takakuwa & Takashima, 1949
= *Mecistocephalus indecorus* Attems, 1901
Prolamnonyx sauteri Silvestri, 1919

Order Scolopendromorpha

Fam. Scolopendridae

Subfam. Scolopendrinae

Scolopendra calcarata Porat, 1876
Scolopendra cingulata Latreille, 1829 - Haase, 1887
Scolopendra mazbii Gravely, 1912 - Zhang & Li, 1983
Scolopendra morsitans L. - Pocock, 1895, Wang, 1955, 1956
Scolopendra mutilans L. Koch 1878 - Pocock, 1895, Brölemann, 1896, Takakuwa, 1938, Wang, 1955
Scolopendra multidens Newport, 1845 - Haase, 1887, Wang, 1955, 1956
Scolopendra rapax Gervais, 1847
Scolopendra rugosa Meinert, 1886
Scolopendra subspinipes Leach, 1817 - Pocock,1895 , Wang, 1955 & auct...
= *Scolopendra septemspinosa* Brandt, 1841- Newport,1845
Scolopendra subspinipes dehaani Brandt, 1840 - Pocock, 1895, Wang, 1955 , 1956
Scolopendra subspinipes japonica L. Koch 1878 - Pocock, 1895, Wang, 1955
Trachycormocephalus koreanus Verhoff, 1934 - Takakuwa, 1938

Subfam. Otostigminae

Otostigmus aculeatus Haase 1887 - Pocock, 1895, Wang, 1955, 1956
Otostigmus insularis (Haase, 1887) - Wang, 1959
Otostigmus malayanus (Chamberlin, 1922) - Wang, 1959
Otostigmus scaber (=*carinatus*) Porat, 1876
Pocock, 1895, Brolemann,1896, Chamberlin & Wang, 1952, Wang, 1955, 1956
Otostigmus politus Karsch, 1881 - Attems, 1901
Otostigmus politus mandschurius Verhoeff, 1942
Otostigmus politus pigmentatus Attems, 1930 - Wang, 1955
Otostigmus striatus Takakuwa, 1940
Otostigmus striatus porteri Dobroruka, 1960
Otostigmus multispinosus Takakuwa, 1937
Otostigmus astenus (Kohlrausch, 1881) - Wang, 1955
Otostigmus frigidus Verhoeff, 1942
Otostigmus frigidus takakuwai Verhoeff, 1942
Rhysida mandchurica Miyoshi, 1939
Rhysida nuda nuda Newport, 1845 - Wang, 1959

Source : MNHN, Paris

Rhysida nuda brevicornuta Wang, 1951 - Wang, 1957
Rhysida nuda immarginata (Porat, 1876) - Wang, 1955, 1957
Rhysida longipes (Newport, 1845) - Wang, 1956
Rhysida longipes brevicornis Takakuwa, 1934 - Takakuwa,1938 et Wang, 1957
Rhysida yanagiharai Takakuwa, 1935
Rhysida lithobioides (Newport, 1845)

Fam. Cryptopsidae

Subfam. Cryptopsinae

Cryptops nigropictus Takakuwa, 1936 - Takakuwa, 1938, Wang, 1956
Cryptops japonicus Takakuwa, 1934 - Chamberlin & Wang, 1952, Takakuwa, 1938
Mimops orientalis Kraepelin, 1903

Subfam. Scolopocryptopsinae

Scolopocryptops brolemanni Kraepelin, 1903
Otocryptops rubiginosa L.Koch, 1878 = O. confucii Karsch, 1884
Otocryptops sexspinosus Say, 1821 - Pocock, 1895 , Attems, 1930

Subclass Epimorpha

Order Lithobiomorpha

Fam. Lithobiidae

Subfam. Lithobiinae

Arebius chengsiensis Chamberlin & Wang, 1952
Areebius bidens Takakuwa, 1941 - Wang, 1952
Chinobius chekianus Chamberlin & Wang, 1952
Chinobius chekianus tumeopes Chamberlin & Wang, 1952 - Wang, 1955, 1956....
Chinobius svenhedini (Verhoeff, 1933)
Chinobius sachalinus Verhoeff, 1937 - Wang, 1956, 1959
Chinobius (?) *pachypedatus* Takakuwa, 1938 - Wang, 1954
Lithobius hummeli (Verhoeff, 1933)
Lithobius bidivisa Takakuwa, 1939 - Wang, 1963
Lithobius kiayiensis Wang, 1959
Lithobius ongi Takakuwa, 1941 - Wang, 1959
Lithobius trichopus Takakuwa, 1939 - Wang, 1955, 1959
Lithobius tetrophthalmus Loksa, 1960
Lithobius aeruginosus mongolicus Attems, 1901
Lithobius decessus Attems, 1901
Lithobius jangsteanus Verhoeff, 1942 - Loksa, 1965
Lithobius kansuanus Verhoeff, 1933
Lithobius mongolicus Verhoeff, 1933
Lithobius erratus Attems, 1938
= *Chinobius* (?) *sulcipes* Attems, 1934 - Wang, 1959
Lithobius bogdoulensis Loksa, 1965
Lithobius anornatus Loksa, 1965
Lithobius mongolellus Loksa, 1965
Lithobius mongolomedius Loksa, 1965
Lithobius sulcifemoralis Takakuwa in Takakuwa & Takashima, 1949
Lithobius gantoensis Takakuwa in Takakuwa & Takashima, 1949
Lithobius irregularis Takakuwa in Takakuwa & Takashima, 1949
Lithobius rufus Muralevitch, 1929 - Loksa, 1965
Monotarsobius crassipes L. Koch, 1862 - Wang, 1963
Monotarsobius crassipes holstii (Pocock, 1895) - Wang, 1959
Monotarsobius rhysus (Attems, 1934) - Chamberlin & Wang, 1952
Monotarsobius argaeensis (Attems, 1905) - Chamberlin & Wang, 1952
Monotarsobius obtusus Takakuwa, 1941 - Wang, 1955, 1956
Monotarsobius ramulosus Takakuwa, 1941 - Wang, 1955, 1956
Monotarsobius alticus Loksa, 1965
Monotarsobius crassus Loksa, 1965
Monotarsobius kaszabi Loksa, 1965

Subfam. Ethopetolidae (=Polybothridae)

Bothropolys asperatus L.Koch, 1878 - Chamberlin & Wang, 1952, Takakuwa, 1938, Wang, 1956
= *Lithobius tethidis* Karsch, 1880

Source : MNHN, Paris

= *Lithobius asperatus* L. Koch, 1878 - Pocock, 1895
= *Lithobius rugosus* Meinert, 1872 - Attems, 1901
Bothropolys crassidentatus Takakuwa in Takakuwa & Takashima, 1949
Bothropolys imaharensis (Verhoeff, 1937)
Takakuwa, 1938, Chamberlin & Wang, 1952, Wang, 1959
Bothropolys richthofeni Verhoeff, 1938 - Takakuwa & Takashima, 1949
Bothropolys shansiensis Takakuwa in Takakuwa & Takashima, 1949
Fam. Henicopidae
Alaskobius takakuwai Chamberlin & Wang, 1952
Esastigmatobius longicornis (Takakuwa, 1936) - Wang, 1959
Esastigmatobius longitarsis Verhoeff, 1934 - Wang, 1959
Hedinobius hummeli Verhoeff, 1933
Lamyctes gracilipes Takakuwa, 1941 - Wang, 1957
Fam. Pterygotergidae
Pterygotergum svenhedini Verhoeff, 1933
Order Scutigeromorpha
Fam. Scutigeridae
Scutigera coleoptrata L. - Wang, 1959
Scutigera sinuata Haase, 1887
Scutigera complanata Haase, 1887
Scutigera hispida Haase, 1887 - Attems, 1901
Thereuopoda clunifera Wood, 1862
= *Scutigera longicornis clunifera* (Wood, 1862) - Pocock, 1895, Chamberlin & Wang, 1952 - Wang, 1955, 1956
= *Scutigera sinensis* Meinert, 1886
Thereuopoda nivicomes Verhoeff, 1942
Thereuonema tuberculata Wood, 1862 - Pocock, 1895
Thereuonema variata Miyoshi, 1939
Thereuonema mandschuria Verhoeff, 1936 - Chamberlin & Wang, 1952, Takakuwa, 1938
Thereuonema dilatationis Verhoeff, 1936 - Takakuwa & Takashima, 1949
Thereuonema hilgendorfi Verhoeff, 1905 - Chamberlin & Wang, 1952, Takakuwa, 1938
Thereuonema viridescens Verhoeff, 1937 - Chamberlin & Wang, 1952

Class PAUROPODA

Ectomorphes
Fam. Pauropodidae
Allopauropus ovalapendicis Zhang & Chen, 1988
Allopauropus pilosisphaerus Zhang & Chen, 1988
Pauropus bifurcus Zhang & Chen, 1988
Pauropus longiramus Zhang & Chen, 1988
Fam. Polypauropidae
Fagepauropus hesperius Remy, 1951 - Chalupsky, 1972
Endomorphes
Fam. Eurypauropodidae
Subfam. Eurypauropodinae
Eurypauropus sp. Zhang & Chen, 1988
Subfam. Sphaeropauropinae
Sphaeropauropus sp. Zhang & Chen, 1988

Class SYMPHYLA

Fam. Geophilellidae
Geophilella pyrenaica Ribaut, 1913 - Takashima, 1939
Fam. Scutigerellidae
Scutigerella immaculata (Newport, 1845) - Wang, 1957

Source : MNHN, Paris

COLLECTING LOCALITIES

Figure 1 shows approximatively the locations of sites in China where myriapods have been collected, during the modern period. In some cases, one single symbol represents several nearby localities. It is obvious that most of the sampling efforts have been concentrared in the south of China. The map unfortunately does not show the intensity of collecting; how many species are known from a given locality? This information cannot be provided until all of the groups of the specimens in the Institute of Zoology of Academia Sinica have been worked out in detail. The collection was mainly taken by LI Zhi-Yin and WANG Daqing from 1969 to 1992 in China.

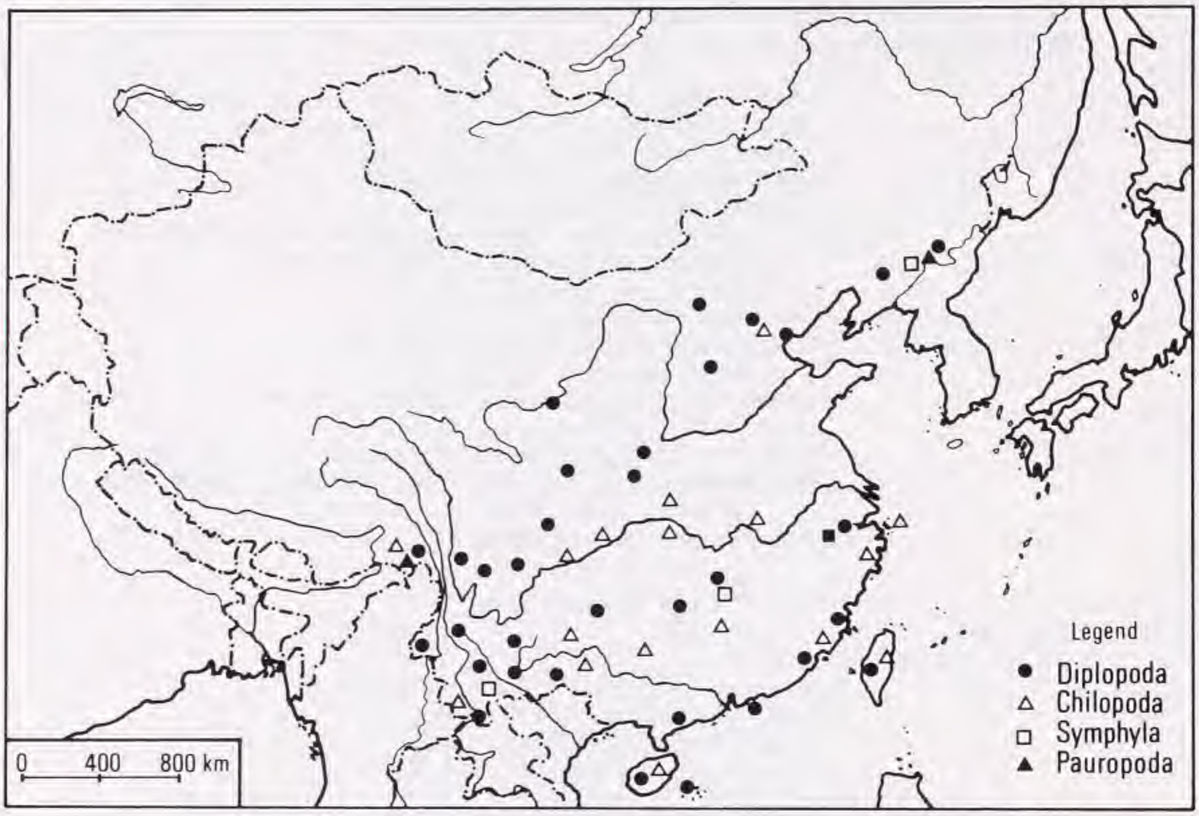


FIG. 1. — Localities in China at which myriapods have been collected. Some closely adjacent sites are represented by single symbols. Due to lack of available material, the geographic coordonates are not given for the following localities. Undoubtedly, some omissions have occured because a few places could not be located exactly, particularly when the localities are small villages: Diao Luo Mountain, Hainan Island - Fuzhou, (vicinity of the city), Fujan province - Yiang shou, a region of the city Gui Lin, Guangxi province - Tian cun, Guangxi province - Mengman, Yunnan province - Luxi, Yunnan province - Jinhua, Zhejiang province - Hong Kang - Jilong, Taiwan - Zhangjakou, Hebei province - Beijing, (vicinity of the city) - Tanmo Mountain, Zhejiang province - Daishan, Zhejiang province - Lanzhou (vicinity), Gansu province - Tai Bai Mountain, Shannxi province - Kunming, Yunnan province - Guanlin (in the caves), Gueizhou province - Hangzhou, Zhejiang province - Chayu, Tibet - Shenyang (vicinity), Liaoning province - Muotuo, Tibet - Chang Bai Mountain, Jilin province - Ningbo, Zhejiang province - Putuo, Zhejiang province - Changsha (vicinity), Hunan province - Yulushan, a hill of Changsha vicinity - Mengla, Yunnan province - Hekou, Yunnan province - Xichou, Yunnan province - Mengzi, Yunnan province - Zhongdian, Yunnan province - Deqin, Tibet - Yiajiang, Sichuan province - Batang, Sichuan province - Taigu, Shanxi province - Zhousha Islands, Zhejiang province - Jiangle, Mt. longxi, Fujian province - Taibei, Taiwan - Taizhong, Taiwan - Pingdong, Taiwan - Zhangjiajie, National Forest Park, Hunan province-Sangzhi, Hunan province - Huhehot, Inner Mongolia - Tianjin(vicinity), Hebei province.

Source : MNHN, Paris

REFERENCES

The aim of the following list of references is to compile all the papers that have been published concerning Chinese myriapodology, including those in wich were described taxa previously found out of China (*) and some ones of general interest (**). Any omissions which may be discovered will be added in future works.

ATTEMS, C., 1898. — System der Polydesmiden I. Denks. *Math.-naturwiss. Kais. Akad. Wiss.*, Wien : 221-482.

ATTEMS, C., 1901. — Myriopoden. *In* : *Dritte Asiatische Forschungreise des Grafen Eugen Zichy, Bd.* 2, Horvath : 275-310.

*ATTEMS, C., 1901. — Neue Polydesmiden des Hamburger-Museums. *Mitt. Naturhist. Mus.*, **18** : 85-105

*ATTEMS, C., 1904. — Central-und hoch-asiatische Myriopoden gesammelt im Jahre 1900 von Dr von Almassy und Dr. von Stummer. *Zool. Jahrb., Syst.*, **20** : 113-130

*ATTEMS, C., 1905. — Myriopoden in Ergebnisse einer naturwissenschaftlichen Reise zum Erschias-Dagh (Kleinasien). *Ann. k.k. Naturh. Hofmuseums*, **20** : 1-5

*ATTEMS, C., 1907. — Japanische Myriopoden gesammelt von Direktor Dr K. Kraepelin im Jahre 1903. *Mitt. Naturh. Mus.*, **24** : 77-142.

*ATTEMS, C., 1909. — Die Myriopoden der Vega-Expedition. *Arkiv f. Zool.*, **5** :1-84.

ATTEMS, C., 1927. — 2. Neue Chilopoden. *Zool. Anz.*, **72** : 291-305.

*ATTEMS, C., 1928. — Eine neue Gattung und eine neue Art der Mecistocephalidae (Chilopoden). *Zool. Anz.*, **75** :115-120.

ATTEMS, C., 1929. — Myriapoda 1. Geophilomorpha. *In* : F. E. SCHULZE & W. KÜKENTHAL, *Das Tierreich*, **52**. Berlin & Leipzig, W. De Gruyter & C° : 1-388.

ATTEMS, C., 1930. — Myriapoda 2. Scolopendromorpha *In* : F. E. SCHULZE & W. KÜKENTHAL, *Das Tierreich*, **54**, Berlin & Leipzig, W. De Gruyter & C° : 1-308.

ATTEMS, C., 1931. — Die Familie Leptodesmidae und andere Polydesmiden. *Zoologica*, **30** : 1-150.

ATTEMS, C., 1934. — Einige neue Geophiliden und Lithobiiden des Hamburger Museums. *Zool. Anz.*, **107** : 310-317.

ATTEMS, C., 1935. — Myriopoden von Sumatra. *Arch. Hydrobiol.*, **suppl. 14** : 114-142.

ATTEMS, C., 1936. — Diplopoda of India. Mem. *Indian Mus.*, **11**, 4 : 133-323.

ATTEMS, C., 1937. — Myriapoda 3. Polydesmoidea. I. Fam. Strongylosomidae. *In* : F. E. SCHULZE, W. KÜKENTHAL & K. HEIDER, *Das Tierreich*, **68**, Berlin & Leipzig, W. de Gruyter & C° : 1-300.

ATTEMS, C., 1938. — Die von Dr. G. Dawydoff in französisch Indochina gesammelten Myriapoden. *Mém. Mus. natn. Hist. nat.*, **6** :187-353.

ATTEMS, C., 1953. — Myriapoden von Indochina Expedition von C. Dawydoff (1938-1939). *Mém. Mus. natn. Hist. nat.*, **A5** : 133-230.

*BRANDT, J. F., 1840. — Observations sur les espèces qui composent le genre *Scolopendra* suivies de caractères des espèces qui se trouvent dans le Muséum Zoologique de l'Académie des Sciences de Saint-Pétersbourg et quelques coups d'œil sur leur distribution géographique. *Bull. Sci. Acad. Saint-Petersbourg*, 7.

BRÖLEMANN, H. W., 1896. — Sur quelques Myriapodes de Chine. *Mém. Soc. zool. France.* : 349-362.

CAUSEY, N. B., 1966. — Redescription of two Chinese species of *Anaulaciulus* (Diplopoda, Julida, Nemasomatidae) a genus known also in Taiwan, Korea and Japan. *Proc. Louis. Acad. Sci.*, **29** : 63-66.

CHALUPSKY, J., 1972. — A new find of the genus *Fagepauropus* (Pauropoda). *Vestnik Cesk. Spolecn. Zool.*, **2** : 89-92.

*CHAMBERLIN, R. V., 1914. — Notes on Chilopods from the East Indies. *Entom. News Philadelphia*, **25** : 385-392.

*CHAMBERLIN, R. V., 1920. — On the Chilopods of the family Mecistocephalidae. *Canad. Entom.*, **52** : 184-189

CHAMBERLIN, R. V., 1923. — Two Diplopod immigrant taken at Honolulu. *Proc. Biol. Soc. Washington*, **36** : 165-168.

CHAMBERLIN, R. V., 1952. — Geophiloid Chilopods of the Hawaian and other Oceanic islands of the Pacific. *Gr. Basin Nat.*, **13** : 75-85

CHAMBERLIN, R. V. & WANG, Y. M., 1952. — Some records and descriptions of Chilopods from Japan and other oriental areas. *Proc. Biol. Soc. Wash.*, **65** : 177-186.

CHAMBERLIN, R. V. & WANG, Y. M., 1953. — Records of Millipeds from Japan and other oriental areas, with description of new genera and species. *Amer. Mus. Novitates*, **1621** : 1-13.

CHANG, N. G. & ZHANG, C. Z., 1989. — A contribution to knowledge of the genus *Yunnanina* and a new species in Yunnan province (Diplopoda Paradoxosomatidae). *Acta Zootaxonomica Sinica*, **14** : 415-419.

CHEN, J. X. & ZHANG, C. Z., 1990. — A cave-dwelling new species of the Diplopod genus *Epanerchodus* from Guizhou province. *Acta Zootaxonomica Sinica*, **15** : 407-409.

Source : MNHN, Paris

CHEN, J. X. & MENG, W. X., 1991. — A new species of the genus *Glyphiulus* (Diplopoda, Spirostreptida, Cambalopsidae). *Acta Zootaxonomica Sinica*, **16** : 394-395.

CHIA , L. P. & LIU, H. T., 1951. — Fossil Myriapods from Choukoutien. *Bull. Geol. Soc. China*, **30** : 23-27.

COOK, O. F. & LOOMIS, H. F., 1924. — A new family of spined Millipeds from Central China. *J. Wash. Acad. Sci.*, **14** : 103-108.

DEMANGE, J. M., 1962. — Matériaux pour servir à une révision des Harpagophoridae (Myriapodes-Diplopodes). *Mém. Mus. natn. Hist. nat., sér. A, Zool.*, **24**, (1961) : 1-274.

DOBRORUKA, L. J., 1960. — A new formosan Centipede: *Otostigmus striatus porteri* n.sp. *Ann. Mag. Nat. Hist.*, **13** : 61-62.

DOBRORUKA, L. J., 1960. — Ueber eine kleine Chilopoden-Ausbeute aus der Mongolei. *Acta Arachnologica*, **17** : 15-18.

ENGHOFF, H., 1985. — The millipede family Nemasomatidae. With the description of a new genus and a revision of *Orinisobates* (Diplopoda: Julida). *Ent. Scand.*, **16** : 27-67.

ENGHOFF, H., 1987. — *Karteroiulus niger* Attems, 1909, in China (Diplopoda, Julida, Paraiulidae). *Entom. Monthly Mag.*, **123** : 207-208.

ENGHOFF, H., 1987. — Revision of *Nepalmatoiulus* Mauriès 1983, a southeast Asiatic genus of Millipedes (Diplopoda: Julida: Julidae). *Courier Forsch.-Inst. Senckenberg*, **93** : 241-331.

GOLOVATCH, S. I., 1978. — Some east-asiatic Millipedes (Diplopoda) in collection of the Zoological Institut of the Academy of Sciences of USSR. *Rev. Entom. , USSR*, **3** : 677-681.

GOLOVATCH, S. I., 1981. — Some East-asiatic millipedes (Diplopoda) in the collection of the Institute of Zoology of the Polish Academy of Sciences. *Ann. Zool.*, **36** : 161-168.

GOLOVATCH, S. I., 1991. — The millipede family Polydesmidae in southern Asia, with notes on phylogeny (Diplopoda: Polydesmidea). *Steenstrupia*, **17** : 141-159

GOLOVATCH, S. I. & HOFFMAN R. L., 1989. — Identity of *Polydesmus hamatus* Brandt, 1841, a Malagasy milliped (Diplopoda, Polydesmida, Dalodesmidae). *Tropical Zool.*, **2** : 159-164.

GERVAIS, P., *In* WALCKENAER, 1847. — *Histoire Naturelle des insectes aptères T.4. Myriapodes. Nouvelles suites à Buffon*, Paris, Librairie Encyclopédique : 1-333.

GRAVELY, F. H., 1912. — Two new species of Scolopendridae. *Rec. Indian Mus.*, **7** : 415-417.

GRESSITT, J. L., 1941. — New Myriopods from Formosa and Hainan Islands. *Ann. Mag. Nat. Hist.*, **11** : 55-61.

HAASE, E., 1887. — Die indo-australische Myriopoden. I. Chilopoden. *Abh. Ber. K. Zool. Anthrop. Mus. Dresden*, **1886-1887** : 1-118.

HOFFMAN, R. L., 1956. — Studies on some oriental xystodesmine millipeds. *Proc. Ent. Soc. Wash.*, **58** : 95-104.

HOFFMAN, R. L., 1961. — Two new Diplopod genera from western China (Polydesmida, Strongylosomidae). *Ann. Mag. Nat. Hist.*,1960, *ser. 13*, **3** : 533-543.

HOFFMAN, R. L., 1963. — A contribution to the knowledge of asiatic Strongylosomoid Diplopoda (Polydesmida, Strongylosomidae). *Ann. Mag. Nat. Hist.*, 1962, *ser. 13*, **5** : 577-593.

HOFFMAN, R. L., 1964. — A new subfamily of Xystodesmid Millipeds from North America and China (Polydesmida). *Trans. Amer. Ent. Soc.*, **90** : 301-311.

HOFFMAN, R. L., 1966. — The ordinal position of the generic name *Sinostemmiulus* Chamberlin & Wang, 1953. *Proc. Ent. Soc. Wash.*, **68** : 322-325.

HOFFMAN, R. L., 1973. — Descriptions and allocation of new or poorly known genera and species of Paradoxosomatidae from south-eastern Asia (Diplopoda: Polydesmida). *J. Nat. Hist.*, **7** : 361-389.

**HOFFMAN, R. L., 1980. — *Classification of the Diplopoda.* Genève, Muséum d'Histoire Naturelle (1979) : 238 pp.

HOFFMAN, R. L., 1980. — Studies on Spirostreptoid millipeds. XV. On some new or poorly known Harpagophorid genera and species from China and the East Indies. *J. Nat. Hist.*, **14** : 589-596.

ISHII, K., 1990. — Penicillate Diplopods (Diplopoda: Polyxenida) from Taiwan. *Edaphologia*, **42** : 1-20.

ISHII, K. & LIANG L., 1990. — Two new species of Penicillate Diplopods of the family Polyxenidae from China. *Cand. Entom.*, **122** : 1239-1246.

JEEKEL C. A. W., 1968. — *On the classification and geographic distribution of the family Paradoxosomatidae (Diplopoda, Polydesmida).* Amsterdam : 1-162.

JEEKEL C. A. W., 1971. — Nomenclator generum et familiarum Diplopodorum. *Monogr. Nederl. Entom. Ver., Amsterdam*, **5 : I-XII, 1-412.

JEEKEL C. A. W., 1980. — The generic allocation of some little-known Paradoxosomatidae from South-East Asia (Diplopoda, Polydesmida). *Rev. Suisse Zool.*, **87** : 651-670.

KARSCH, F., 1880. — Ein neuer *Lithobius*. *Zeitschr. f. Ges. Naturwiss.*, **53** : 848.

Source : MNHN, Paris

KARSCH, F., 1881. — Zur Studium der Myriapoda Polydesmida I. Diagnosen neuer Polydesmiden des Berliner Museum. *Archiv f. Naturges.*, **47** : 36-43.

KARSCH, F., 1881. — Neue Juliden des Berliner Museums, als Prodromus einer Juliden-Monographie. *Zeitschr. f. Ges. Naturwiss.*, **54** : 1-79.

KARSCH, F., 1884. — Classis Myriapoda. *In* : Ueber einige neue und minder bekannte Arthropoden des Bremer Museums. *Abh.Ver. Bremen*, **9** : 65-67.

KEETON, W. T., 1960. — A taxonomic study of the milliped family Spirobolidae (Diplopoda, Spirobolida). *Mem. Amer. Entom. Soc.*, **17** : 1-146.

*KOCH, C. L., 1847. — *System der Myriapoden III.* Regensburg.

*KOCH, L., 1862. — Die Myriapodengattung *Lithobius.* Nürnberg : 1-92.

KOCH, L., 1878. — Japanesische Arachniden und Myriapoden. *Verh. d. k. k. Zool. Bot. Ges. Wien*, 1877, **27** : 735-798.

*KOHLRAUSCH, E., 1881. — Gattungen und Arten der Scolopendriden. *Arch. F. Naturges.*, **47** : 50-132.

KRAEPELIN, K., 1903. — Revision der Scolopendriden. *Mitt. Naturh. Mus. Hamburg*, **20** : 1-276.

*LEACH, W. E., 1817. — A tabular view of the external characters of four classes of animals, which Linné arranged under insecta; with the distribution of the genera composing three of the Classes into Orders, and description of several new genera and species. *Trans. Linn. Soc. London*, **11**, (1814) : 306-400.

LI, Z. Y. & ZHANG, C. Z., 1980. — The individual development of *Scolopendra subspinipes mutilans* (Scolopendrida, Chilopoda). *Chinese J. Zool.*, **15** : 17-19.

LI, Z. Y. & ZHANG, C. Z., 1982. — Experimental studies on the increase in the breeding rate of *Scolopendra subspinipes mutilans* by use of the artificial nest. *Chinese J. Zool.*, **17** : 27-30.

LI, Z. Y., 1984. — The species of medicinal centipeds and the selection of their breeding. *Chinese J. Zool.*, **19** : 12-15.

LIN, P. S. & DOUY, L. H., 1988. — The toxicological experiment of toxin taken from *Scolopendra mutilans*. *Chinese J. Zool.*, **23** : 20-21.

LOKSA, I., 1960. — Einige neue Diplopoden und Chilopoden-Arten aus Chinesischen Höhlen. *Acta Zool. Hungar.*, **6** : 135-148.

LOKSA, I., 1965. — Zoologische Ergebnisse der Forschungen von Dr Z. Kaszab in der Mongolei. 21. Chilopoda. *Opusc. Zool.* , **5** : 199-215.

LOKSA, I., 1978. — Chilopoden aus der Mongolei (Arthropoda: Tracheata, Chilopoda). *Ann. Hist. Nat. Mus. Nat. Hung.*, **70** : 111-120.

LOOMIS, H. F., 1942. — *Sinocybe*, a new genus of Colobognath millipeds from China. *J. Wash. Acad. Sci.*, **32** : 270-273.

*LUCAS, H., *In* MAILLARD, 1863. — Myriapodes. *In* : Note sur l'Ile de La Réunion.

MATIC, Z., 1973. — Révision du genre *Chinobius* Verhoeff, avec description de trois espèces nouvelles (Chilopoda, Lithobiida). *Ann. Zool. Pologne*, **30** : 33-47.

*MEINERT, F., 1872. — Myriapoda Musaei Hauniensis. *Naturh. Tidsskr.* : 281-344.

MEINERT, F., 1886. — Myriapoda Musaei Hauniensis. *Vid. Medd. f. d. naturh. Foren. i Kjobenhavn*, (1884) : 100-156.

MEINERT, F., 1886. — Myriapoda Musaei Cantabrigensis. Part I. Chilopoda. *Proc. Amer. Phil. Soc.*, (1885), **23** : 161-233.

MIYOSHI, Y., 1939. — Chilopoda. *In* : *Report of the first Scientific Expedition to Manchoukuo under the leadership of Shigeyasu Tokunaga, June-Oct. 1933*, 5, 1, 14, n°**77** : 1-26.

*MIYOSHI, Y., 1951. — Beiträge zur Kenntnis japanischer Myriopoden. 1. Aufsatz: Ueber eine Gattung von Leptodesmidae. *Zool. Mag. Tokyo*, **60** : 149-150.

*MURALEVITCH, V. S., 1929. — Scutigeridae et Lithobiidae de la faune du Caucase. *Mém. Soc. Amis Sci. Nat. Moscou , Zool.* : 1-120.

NEWPORT, G., 1845. — XXVIII. Monograph of the class Myriapoda, order Chilopoda; with observations on the general arrangement of the Articulata. *Trans. Linn. Soc. London*, (1844), **19** : 349-438.

*NGUYEN DUY - JACQUEMIN, M. & CONDÉ, B., 1982. — Lophoproctides insulaires de l'Océan Pacifique (Diplopodes: Penicillates). *Bull. Mus. natl. Hist. nat.* , Paris, **4** : 95-118.

POCOCK, R. L., 1895. — Report upon the Chilopoda and Diplopoda obtained by P. W. Bassett-Smith and J. J. Walker during the cruise in the Chinese Seas of H. M. S. Penguin. *Ann. Mag. Nat. Hist.*, **6** : 346-372.

POCOCK, R. L., 1895. — The Myriapoda of Burma. Pt. IV. Report upon the Polydesmoidea collected by S. L. Fea, M. E. W. Oates and others. Viaggio di Leonardo Fea in Birmania e regione vicine. *Ann. Mus. civ. Stor. nat. Genova, ser. 2a*, 14, **34** : 787-834.

PORAT, C. O., 1876. — Om nagra exotiska Myriopoder. *Sven. Vet. Akad. Handlingar*, **4** : 1-48.

Source : MNHN, Paris

*REMY, P., 1951. — Un nouveau type de Pauropode: *Fagepauropus hesperius* n. g., n. sp. du Sud-marocain. *Bull. Mus. natl. Hist. nat., Paris*, 2 , **23** : 208-210.

*RIBAUT, H., 1913. — Un nouveau genre de la Classe des Symphyles (Myriopodes). *Bull. Soc. Hist. nat. Toulouse*, **14** : 77-84.

*SAUSSURE, H. de, 1860. — *Essai d'une Faune des Myriapodes du Mexique. Mémoires pour servir à l'Histoire naturelle du Mexique, des Antilles et des Etats-Unis*. Genève : 1-135.

*SAY, E., 1821 . — Description of the Myriapoda of the United States. *J. Acad. Nat. Sci. Philad., 1° ser.*, **2** : 102-114.

*SELIVANOV, A., 1881. — Geophilidae Museja imperatorskoi. *Mém. Acad. Imp. Sci. Saint-Péterbourg*, **7**.

SELIVANOV, A., 1881. — Neue Lithobiiden aus Sibirien und Central Asien. *Zool. Anz.* , **4** : 15-17.

SHEAR, W. A., 1990. — On the Central and East Asian Milliped family Diplomaragnidae (Diplopoda, Chordeumida, Diplomaragnoidea). *Amer. Mus. Novitates*, **2977** : 1-40.

*SILVESTRI, F., 1898. — Alcuni nuovi Diplopodi della N. Guinea. *Annali Mus. civ. Stor. nat. G. Doria*, **39** : 441-449.

*SILVESTRI, F., 1910. — Descrizioni preliminari di nuovi generi di Diplopodi I. Polydesmoidea. *Zool. Anz.*, **35** : 357-364.

SILVESTRI, F., 1919. — Contributions to the knowledge of the Chilopoda Geophilomorpha of India. *Records Indian Mus.*, **16** : 45-107.

SILVESTRI, F., 1948. — Contributo alla conoscenza dei Diplopodi termitofili dell'America meridionale. *Boll. Lab. Entom. agraria Portici*, **8** : 1-32.

*TAKAKUWA, Y., 1934a. — Sechs neue Arten der Chilopoden aus Japan. *Trans. Sapporo Nat. Hist. Soc.*, **13** : 398-406.

TAKAKUWA, Y., 1934b. — Ueber drei neue Arten der Chilopoden aus Formosa und Marschallinseln. *Trans. Nat. Hist. Soc. Formosa*, **24** , n°132 : 221-225.

*TAKAKUWA, Y., 1935a. — Ueber neue Chilopoden aus Japan. *Trans. Nat. Hist. Soc. Formosa*, **25**, n° 145 : 339-342.

*TAKAKUWA, Y., 1935b. — [Japanese *Escaryus* (Chilopoda)]. *Dobuts. Zasshi*, **47**, n° 561: 407-411.

TAKAKUWA, Y., 1936a. — Eine neue interessante *Mecistocephalus*-Art aus Formosa. *Trans. Nat. Hist. Soc. Formosa*, **26** , n° 152 : 215-216.

TAKAKUWA, Y., 1936b. — Ueber eine neue Gattung und zwei neue Arten von Mecistocephalidae aus Formosa. *Trans. Nat. Hist. Soc.Formosa*, **26** , n° 159 : 435-439

TAKAKUWA, Y., 1936c. — Ueber eine neue Subspecies der *Ethmostigmus* aus Marshallinseln und eine neue spezies der *Nodocephalus* aus Mandschurei. *Trans. Nat. Hist. Soc. Formosa*, **26**, n° 151 : 105-106.

*TAKAKUWA, Y., 1937 . — *Otostigmus*-Arten aus Japan. *Trans. Nat. Hist. Soc. Formosa*, **27**, n° 164 : 221-225.

TAKAKUWA, Y., 1938. — Verzeichnis der Japanischen und Mandschureischen Chilopodenarten. *Annot. Zool. jap.*, **17** : 353-359.

*TAKAKUWA, Y., 1939. — Über Japanische Lithobius-Arten. *Trans. Sapporo Nat. Hist. Soc.*, **16** : 28-37.

*TAKAKUWA, Y., 1940a. — Eine neue *Nodocephalus* Arten (Chilopoda) aus Korea. *Trans. Nat. Hist. Soc. Formosa*, **30**, n° 197-198 : 41-42.

TAKAKUWA, Y., 1940b . — Eine neue Art von *Otostigmus* (Chilopoda) aus Formosa. *Trans. Nat. Hist. Soc. Formosa*, **30**, n° 200-201 : 209-210.

TAKAKUWA, Y., 1940c . — Ueber zwei neue *Trigoniulus*-Arten (Diplopoda) aus Taiwan. *Trans. Nat. Hist. Soc. Formosa*, **30**, n° 200-201 : 211-215.

TAKAKUWA, Y., 1940d. — Weitere *Trigoniulus*-Arten aus Japan (Diplopoda). *Ann. Zool. jap.*, **19** : 283-288.

TAKAKUWA, Y., 1941. — Ueber einige japanische Lithobiiden. *Trans. Nat. Hist. Soc. Formosa*, **31**, n° 213 : 292-297.

TAKAKUWA, Y., 1942a. — Ueber weitere japanische *Rhysodesmus*-Arten. *Trans. Nat. Hist. Soc. Formosa*, **32**, n° 224 : 197-203.

TAKAKUWA, Y., 1942b. — Die Myriapoden von Formosa, Philippinien, u.s.w. *Trans. Nat. Hist. Soc. Formosa*, **32**, n° 231 : 359-367.

TAKAKUWA, Y., 1942c . — 3 n. sp. of Diplopoda from Japan. *Zool. Mag. Tokyo*, **54** : 237-239. (in japanese).

*TAKAKUWA, Y., 1942d. — Zur Kenntnis der japanischen Diplopoden. *Annot. Zool. Jap.*, **21** : 39-47.

TAKAKUWA, Y., 1943. — Die drei neue Diplopoden aus Taiwan und West-nippon. *Trans. Nat. Hist. Soc. Formosa*, **33**, n° 242-243 : 603-606.

TAKAKUWA, Y. & TAKASHIMA, H., 1949. — Myriapods collected in Shansi, North China. *Acta Arachnologica*, **9**, n° 314 : 51-69.

TAKASHIMA, H., 1939. — Diplopoda. *In : Report of the first Scientific Expedition to Manchoukuo under the leadership of Shigeyasu Tokunaga, June-Oct. 1933*, 5 , 1 , **14**, n° 78 : 1-11.

Source : MNHN, Paris

TAKASHIMA, H., 1939 — Symphyla. *In* : *Report of the first Scientific Expedition to Manchoukuo under the leadership of Shigeyasu Tokunaga, June-Oct. 1933*, 5 , 1 , **14**, n° 79 : 1-5.

*VERHOEFF, K. W., 1901. — Zur vergleichende Morphologie, Systematik und Geographie der Chilopoden. *Nova Acta Leopoldina*, **77** : 369-465.

*VERHOEFF, K. W., 1905. — Ueber Scutigeriden. 6. Aufsatz. Variabilität und *Thereuonema*-Arten. Tarsen mit sprungweiser Abänderung. *Zool. Anz.*, **29** : 353-371.

*VERHOEFF, K. W., 1914. — Ascospermophoren aus Japan. *Zool. Anz.* , **43** : 342-370.

*VERHOEFF, K. W., 1928. — Geophilomorphen-Beiträge und eine *Lithobius*-Form. *Mitt. Zool. Mus. Berlin*, **14** : 227-286.

*VERHOEFF, K. W., 1931. — Chilognathen aus den Bergamasker Alpen und Nachbargebieten; aus über zwei neue Gattungen der Polydesmoidea aus Spanien und Japan. *Zool. Jahrb., Syst.*, **61** : 397-452.

VERHOEFF, K. W., 1933. — Schwedisch-chinesische wissenschaftlich Expedition nach den nordwestlichen Provinzen Chinas, unter Leitung von Dr. Sven Hedin und Prof. Su Ping-chang. *Ark. Zool.*, **26** : 1-41.

*VERHOEFF, K. W., 1934. — Beiträge zur Systematik und Geographie der Chilopoden. *Zool. Jarbh., Syst.*, **66** : 1-152.

VERHOEFF, K. W., 1935. — Ueber *Scolioplanes*. *Zool. Anz.*, **111** : 10-23.

VERHOEFF, K. W., 1936a. — Zur Kenntnis der Glyphiuliden (Cambaloidea). *Zool. Anz.*, **113** : 49-62.

VERHOEFF, K. W., 1936b. — Kritische Untersuchung asiatischer Scutigeriden. *Zool. Anz.*, **115** : 1-18.

VERHOEFF, K. W., 1936c. — Ueber Diplopoden aus Japan gesammelt von Herrn Y. Takakuwa. *Trans. Sapporo Nat. Hist. Soc.*, **14** : 148-172.

*VERHOEFF, K. W., 1937a. — Chilopoden aus Malacca nach den Objekten des Raffles Museum in Singapore. *Bull. Raffles Mus. Singapore*, **13** : 198-270.

*VERHOEFF, K. W., 1937b. — Zur Kenntnis der Lithobiiden. *Arch. Naturgesch.*, **6** : 71-257.

*VERHOEFF, K. W., 1938. — Über einige ostasiatische Lithobiiden. *Zool. Anz.*, **123** : 99-105.

VERHOEFF, K. W., 1939a. — Zur Kenntnis ostasiatischer Diplopoden. IV. *Zool. Anz.*, **127** : 273-285.

VERHOEFF, K. W., 1939b. — Diplopoden von den Ryukiu-Insel Okinawa. *Biogeographica*, **3** : 118-122.

VERHOEFF, K. W., 1942a. — Chilopoden aus innerasiatischen Hochgebirgen. *Zool. Anz.*, **137** : 35-52.

VERHOEFF, K. W., 1942b. — Otostigmen der Mandschurei. *Zool. Anz.*, **138** : 181-188.

WANG, D. Q., 1993. — Animals of Jangle Mountain: Diplopoda, Chilopoda. Ed. Huang Chuenmei, China Forestry Publishing House : 855-862.

WANG, D. Q. & ZHANG, C. Z., 1993. — Diplopoda, Chilopoda. Animals of Longqi Mountains, **8** : 845-851.

WANG, D. Q. & ZHANG, C. Z., 1993. — A new Family of Millipeds (Diplopoda, Callipodida) from southwestern China. *Mem. Peking Nat. Hist. Mus.*, **53** : 375-390.

*WANG, Y. M., 1951. — *The Myriapoda of the Philippine Islands*. Ed. Edwards (Ann Arbor, Michigan, USA) : 1-80.

WANG, Y. M., 1955a. — Serica 1a: Records of Myriapods on Formosa with descriptions of new species. *Quart. J. Taiwan Mus.*, **8** : 13-16.

WANG, Y. M., 1955b. — Serica 1b: A preliminary report on Myriapoda and Arachnida of Lan You Islets (Botel Tobago), China. *Quart. J. Taiwan Mus.*, **8** : 195-201.

WANG, Y. M., 1956. — Serica 1e: Records of Myriapods on Formosa with description of new species (2). *Quart. J. Taiwan Mus.*, **9** : 155-159.

WANG, Y. M., 1957a. — Serica 1f : Records of Myriapods on Taiwan Islands (3) Pescadore Islets, Kao-Young, Pingtung, Changhua and Taipei. *Quart. J. Taiwan Mus.*, **10** : 23-29.

WANG, Y. M., 1957b. — Serica 1g : Records of Myriapods on Taiwan Islands (4) Six new Polydesmids. *Quart. J. Taiwan Mus.*, **10** : 103-111.

WANG, Y. M., 1957c. — Serica 1h : Records of Myriapods on Taiwan Islands (5) With descriptions of three new species. *Quart. J. Taiwan Mus.*, **10** : 112-115.

WANG, Y. M., 1958a. — Serica 1i : On Diplopoda from Taiwan with a new Strongylosomid. *Quart. J. Taiwan Mus.*, **11** : 340-344.

WANG, Y. M., 1958b. — Records of Formosan Myriapods. *In* : *Proc. 10th Int. Congr. Ent. Montréal*, **1**, 1956 : 881-882.

WANG, Y. M., 1959. — Serica 1j : On Chilopoda from Taiwan with a new Lithobid. *Quart. J. Taiwan Mus.*, **12** : 195-199.

WANG, Y. M., 1960. — On Millipedes and Centipedes from Taiwan, China. *In* : *Verh. XI. intern. Kongr. Entom. Wien, 17-25 August 1960* : 288-291.

Source : MNHN, Paris

WANG, Y. M., 1961. — Serica 1k: Millipedes of Taiwan. A new species of family Spirobolidae. *Quart. J. Taiwan Mus.*, **14** : 141-142.

WANG, Y. M., 1963a. — Serica 1q: Millipedes and Centipedes of Quemoy, Fukien province and Taiwan Island, Botel Tobago (Lan Yu), Taiwan province and of Singapore. *Quart. J. Taiwan Mus.*, **16** : 89-96.

WANG, Y. M., 1963b. — The Millipedes and Centipedes of Taiwan, China. *In* : *Proc. XVI° Congress Zool. Washington, 1* : 211.

WANG, Y. M., 1964. — Serica 1op: *Wallacea* and insular Fauna of Millipedes. *Quart. J. Taiwan Mus.*, **17** : 67-76.

WANG, Y. M. & WANG T. N. G., 1965. — Distribution of orders Polydesmida and Spirobolida in some oriental islands. *In* : *Proc. XIIth Int. Congress Entom. London, 1964*: : 444-445.

WOOD, H. C., 1863. — On the Chilopoda of North America, with a catalogue of all the specimens in the collection of the Smithsonian Institution. *J. Philad. Acad.*, **5** : 5-52.

WOOD, H. C., 1865. — New Polyzoniidae. *Proc. Acad. Philadelphie*, **17** : 172-173.

ZHANG, C. Z., 1985a. — A new species of millipeds of the genus *Junceustreptus* in Southwestern China. *Acta Zool. Sinica*, **10** : 137-139.

ZHANG, C. Z., 1985b. — A new species of millipeds of the genus *Skleroprotopus* in Stone Buddha Cave, Fangshang County, Beijing. *In* : *Karst Geomorphology and Speleology*. Beijing, Science Press : 154-156.

ZHANG, C. Z., 1986. — On the genus *Pratinus* and its two new species from China. *Acta Zootaxon. Sinica*, **11** : 253-257.

ZHANG, C. Z., 1987a. — A study on decocting methods for *Scolopendra* spp. *Bull. Chin. Mater Med.*, (1986), **11** : 661-663.

ZHANG, C. Z., 1987b. — Breeding biology of medicinal Centipeds. Sci. Press.

ZHANG, C. Z., 1993. — Diplopoda from Yunnan caves (II): Contribution to the study of a new cavernous taxon of the Nematophoran Millipeds (Diplopoda, Cœlocheta, Callipodida). *In* : *Proc. XIth Int. Congress Speleol., August 2-8 1993.* : 128-130.

ZHANG, C. Z., (in press). — An interesting new millipede, *Agariogonopus acrotrifoliatus*, gen. et sp. nov., from a limestone district of Yunnan, China.

ZHANG, C. Z. & CHANG, N. G., 1990. — A new genus and new species of the family Harpagophoridae from Yunnan, China (Diplopoda, Spirostreptoidea). *Acta Zootaxonom. Sinica*, **15** : 32-35.

ZHANG, C. Z. & CHEN, Z. P., 1983. — A new species of the genus *Epanerchodus* (Diplopoda: Polydesmida) from Zhejiang province. *Acta Zhejiang Teacher's College (Nature Sci.)*, **6** : 87-89.

ZHANG, C. Z. & CHEN, Z. P., 1988. — A preliminary study on a new record of the class Pauropoda (Myriapoda) from China. *Sinozoologica*, **6** : 39-54.

ZHANG, C. Z. & JIN, Y. L., 1981. — A textual study on the medicinal Myriapoda in Ben Cao Gang Mu (the Chinese Encyclopedia of material medicine) 1596. *J. Chin. tradition. Medicine*, **478** : 50-56.

ZHANG, C. Z. & LI, Z. Y., 1975. — On the difference between *Spirobolus joannesi* (Brölemann) and *Kronopolites swinboei* (Pocock) used in medicine. *Chinese J. Zool.*, **4** : 29-30.

ZHANG, C. Z. & LI, Z. Y., 1977a. — Eine neue *Yunnanina*-Art (Diplopoda) aus China. *Acta Zool. Sinica*, **23** : 357-359.

ZHANG, C. Z. & LI, Z. Y., 1977b. — A survey of the Centipede used in medicine (*Scolopendra subspinipes multidens* Newport) from Duan County, Guangxi. *Chinese J. Zool.*, **1977,** 2 : 33-34.

ZHANG, C. Z. & LI, Z. Y., 1977c. — Preliminary studies on the centipede (*Scolopendra subspinipes multidens* Newport) from Hubei province. *Chinese J. Zool.*, **1977,** 1 : 34-36.

ZHANG, C. Z. & LI, Z. Y., 1978a. — On medical *Kronopolites svenhedini* (Verhoeff) (Diplopoda, Paradoxosomatidae). *Chinese J. Zool.*, **1978,** 3 : 12-13.

ZHANG, C. Z. & LI, Z. Y., 1978b. — On some Myriapoda from Xisha Islands, Guangdong province. *Chinese J. Zool.*, **1978,** 4 : 1-3.

ZHANG, C. Z. & LI, Z. Y., 1979a. — Studies on the habits and characteristics of *Scolopendra subspinipes mutilans* L. Koch (Chilopoda). *Chinese J. Zool.*, **1979,** 1 : 20-22.

ZHANG, C. Z. & LI, Z. Y., 1979b. — The spawn (observations on egg-laying) of *Scolopendra mutilans* L. Koch. *Chinese J. Zool.*, **1979,** 4 : 13-15.

ZHANG, C. Z. & LI, Z. Y., 1979c. — The habits of *Scolopendra mutilans* L. Koch. *Chinese J. Zool.*, **1979, 4** : 20-22.

ZHANG, C. Z. & LI, Z. Y., 1980a. — A preliminary analysis of structure and product of *Scolopendra mutilans* in Daishan County. *Chinese J. Zool.*, **1980,** 2 : 1-3.

ZHANG, C. Z. & LI, Z. Y., 1980b. — Textual research of medicinal *Spirobolus*. *J. Chin. tradition. Medicine*, **6** : 66-67.

ZHANG, C. Z. & LI, Z. Y., 1981a. — Ueber Bilingulidae fam. nov.(Diplopoda Spirostreptida) aus dem südchinesischen Karstgebiet. *Acta Zool. Sinica*, **6** : 376-377.

Source : MNHN, Paris

ZHANG, C. Z. & LI, Z. Y., 1981b. — Eine neue Art vom *Archandrodesmus* (Cryptodesmidae, Diplopoda). *Acta Zootaxonom. Sinica*, **6** : 250-252.

ZHANG, C. Z. & LI, Z. Y., 1982a. — *Centrodesmus cornutus* sp. nov. eine neue Diplopoden-Art (Paradoxosomatidae, Polydesmida) aus dem Süd-China. *Acta Zootaxonom. Sinica*, **7** : 37-39.

ZHANG, C. Z. & LI, Z. Y., 1982b. — Eine neue Art vom *Chinosphaera* (Spherotheriida, Diplopoda) aus China. *Acta Zootaxonom. Sinica*, **7** : 152-154.

ZHANG, C. Z. & LI, Z. Y., 1982c. — Die Gattung *Glyphiulus* (Diplopoda, Cambalidea) von China. *Sinozoologica*, **2** : 85-93.

ZHANG, C. Z. & LI, Z. Y., 1983. — The *Scolopendra mazbii* Gravely, 1912 of Xizang Autonomus region (Tibet). *Chinese J. Zool.*, **1983,** 5 : 50-51.

ZHANG, C. Z. & LI, Z. Y., 1990. — Textual research of medicinal Polydesmoid. *J. Chin. tradition. Medicine*, **466** : 66-67.

ZHANG, C. Z., LI, Z. Y.& MAO, J. R., 1980. — The preliminary study on Symphyla of China. *Chinese J. Zool.*, **1980,** 2 : 4-7.

ZHANG, C. Z., LI, Z. Y. *et al.* 1983. — The development of *Scolopendra subspinipes mutilans* L. Koch (Scolopendridae, Chilopoda). *Chinese J. Zool.*, **1983,** 4 : 17-19.

ZHANG, C. Z., LI, Z. Y. & MAO, J. R., 1984. — A new species of the genus *Kiulinga* (Diplopoda, Xystodesmidae). *Acta Zootaxonomica Sinica*, **9** : 135-137.

ZHANG, C. Z. & TANG, H.G., 1985. — Eine neue Art der Gattung *Hedinomorpha* (Diplopoda, Paradoxosomatidae) aus China. *Sinozoologica*, **3** : 35-38.

ZHANG, C. Z. & WANG, D. Q., 1993. — Diplopoda from Yunnan caves (I): A study on new genera and species of the millipede family Doratodesmidae. *In* : *Karst landscape & Cave tourism*. China Environ. Sci. Press : 205-220.

ZHANG, C. Z., ZHANG, F. X. & WANG, D. Q., 1992. — A survey on the resources of Centipeds for medicinal use in Wuling Mountains. *Chinese J. Zool.*, **27** : 8-11.

Source : MNHN, Paris

Source : MNHN, Paris

A Taxonomic Study of Polydesmoid Millipedes (Diplopoda) Based on their Mandibular Structures

Kiyoshi ISHII * *and Hiroshi* TAMURA **

* Department of Biology, Dokkyo University School of Medicine, Mibu, Tochigi 321-02, Japan
** Department of Biology, Ibaraki University, Mito, Ibaraki 310, Japan

ABSTRACT

The mandibular structures of 8 families, 25 genera and 34 species of polydesmoid millipedes have been examined based on the material collected from Japan and China. Detailed examinations revealed that the molar structure was especially useful for the taxonomy of this order. The key to the family on the basis of molar structure is also given.

RÉSUMÉ

Etude taxinomique des diplopodes polydesmoïdes basée sur leurs structures mandibulaires.
Les structures mandibulaires de 8 familles, 25 genres et 34 espèces de diplopodes polydesmides ont été examinées à partir du matériel récolté au Japon et en Chine. Des observations détaillées ont montré que les structures "molaires" étaient particulièrement utiles pour l'étude taxinomique de l'ordre Polydesmida. Une clé des familles, basée sur la structure en "molaire", est également proposée.

INTRODUCTION

The mandibular structures of millipedes have so far been treated as minor taxonomic characters since MANTON (1964), while LAUTERBACH (1972) noted function of mandible in millipedes. ENGHOFF (1979, 1981, 1985) and ISHII (1988) discussed on the taxonomic significance of mandibular structures in a few millipede orders. Recently, ISHII & TAMURA (1992) compared mandibles of 9 orders, 22 families, 46 genera and 65 species of millipedes, suggesting usefulness of the mandibles as a diagnostic character in general in millipedes.

The mandibular structures of polydesmoid millipedes were investigated by ENGHOFF 1979, 1985) for only three families and four genera: Polydesmidae, *Brachydesmus* and *Serradium*; Macrosternodesmidae, *Macrosternodesmus* and Oxydesmidae gen.

In this study, we have made an intensive examination on the mandibular structure of 8 families, 25 genera and 34 species (TABLE 1) collected from Japan and China to confirm its extensive usefulness as a taxonomic character throughout Polydesmoid millipedes.

METHODS

Mandibles were removed from the mouthparts using an ophthalmologic knife and forceps under a stereoscopic binocular microscope, and further made clear using a microbrush and fluid pressure. The mandibles were fixed with 80%

ISHII, K. & TAMURA, H., 1996. — A taxonomic study of polydesmoid millipedes (Diplopoda) based on their mandibular structures. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 101-111. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

alcohol, dehydrated in a graded alcohol series, put overnight into isoamyl, and then dried in a critical point drier using liquid carbon dioxide. The dried mandibles were coated with gold and observed with a scanning electron microscope.

TABLE 1. — List of Polydesmoid millipedes species examined.

Fam. Paradoxosomatidae: *Haplogonosoma implicatum, Chamberlinius cristatus, C. haulienensis, Oxidus gracilis, Orthomorpha coarctata, Nedyopus tambanus, Centrodesmus* sp. (unpublished sp. collected from China), undetermined gen. collected from China.

Fam. Xystodesmidae: *Levizonus takakuwai, Parafontaria ishiii, P. laminata armigera, Xystodesmus* sp. (unpublished sp.), *Riukiaria* sp. (unpublished sp.).

Fam. Polydesmidae: *Polydesmus japonicus, Epanerchodus mammillatus, E. orientalis, E.* sp.-1 (unpublished sp.), *E.* sp.-2 (unpublished sp.), *Prionomatis* sp. (unpublished sp.).

Fam. Opisotretidae: *Corypholophus* sp. (unpublished sp.).

Fam. Cryptodesmidae: *Kiusiunum sekii, K. nodulosum, Niponia nodulosa.*

Fam. Pyrgodesmidae: *Ampelodesmus granulosus, Cryptocorypha japonica.*

Fam. Doratodesmidae: *Eucondylodesmus elegans, Kylindogaster nodulosa, Thelodesmus armatus, T.* sp. (unpublished sp.), *Dimorphodesmus* sp.-1 (unpublished sp.), *D.* sp.-2 (unpublished sp.),*D.* sp.-3 (unpublished sp.), undetermined gen. collected from China.

Fam. Haplodesmidae: *Rhipidopeltis* sp. (unpublished sp.).

GENERAL MORPHOLOGY OF THE MANDIBLE OF POLYDESMOID MILLIPEDES

General morphology of the mandible of millipedes has been mentioned by ATTEMS (1937), MANTON (1964), ENGHOFF (1979), ISHII (1988), ISHII & TAMURA (1992), and HOPKIN & READ (1992). The general morphology of mandibles of Polydesmoid millipedes are shown in Figure 1. The mandible is composed of 4 parts: 1) the proximal plate, armed with molar plate consisting of wide or narrow molar processes, molar comb between molar process, molar hook, molar tuft at proximal end, fringe, and granulated zone; 2) the intermediate plate, armed internally with intermediate lobe covered by scaly hairs; 3) comb-lobe, with six rows of comb teeth; 4) internal tooth and external tooth. Both molar plates has a muller as showed in Figures 1-4.

RESULTS AND DISCUSSION

The mandible of Polydesmoid millipedes is characterized by extremely stout external and internal teeth and comb teeth arranged in six rows, and also by crescent or triangular molar plate with wide or sawtooth roof-like molar process, molar tuft at proximal end and lamellate fringe or branched fringe at apex.

The external tooth of mandible is simple in the families Paradoxosomatidae and Xystodesmidae (Fig. 2). Other families such as Polydesmidae, Opisotretidae, Cryptodesmidae, Doratodesmidae, Pyrgodesmidae and Haplodesmidae have one or two lateral denticles. The families Opisotretidae, Haplodesmidae and Pyrgodesmidae have a node.

The internal tooth is marginally divided into four to seven leaflets. The number of leaflets and depth of emargination are varied depending on genus and/or species. Therefore, we assume that the structures of both external and internal teeth are important diagnostic characters for lower taxa rather than the family.

The intermediate lobe is less developed except the family Pyrgodesmidae in comparison with the other millipedes orders such as Penicillata, Spirostreptida, Chordeumatida and Julida.

The molar structure of mandible is most stable within diagnostic characters of the family of polydesmoid millipedes. The molar structures are given below for the 8 families examined in this study.

Source : MNHN, Paris

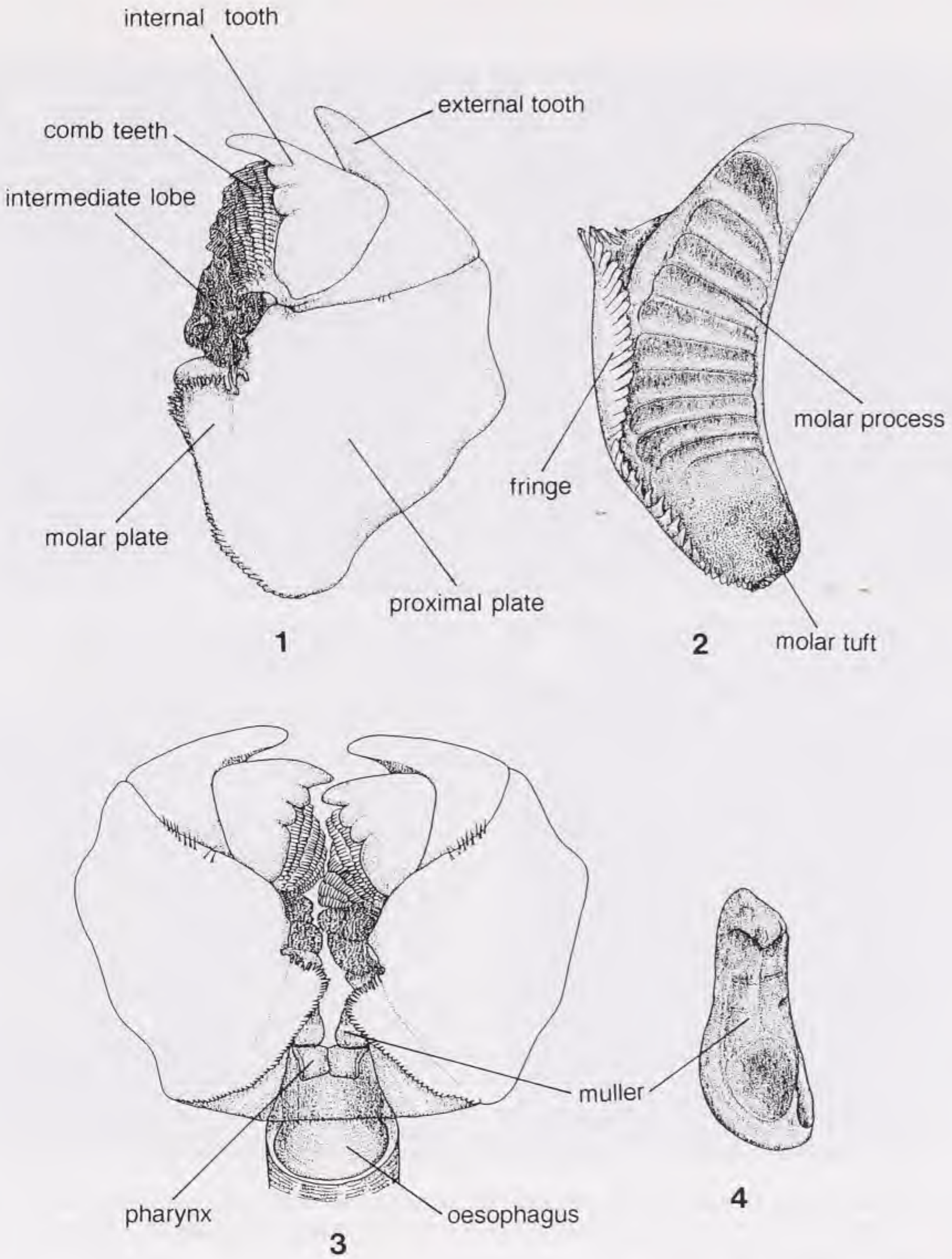


FIG. 1. — The mandibular structure of *Parafontaria laminata armigera*. 1, right mandible (dorsal view); 2, molar plate (internal view); 3, disposition of mandible, muller, pharynx and oesophagus (dorsal view); 4, muller.

Source : MNHN, Paris

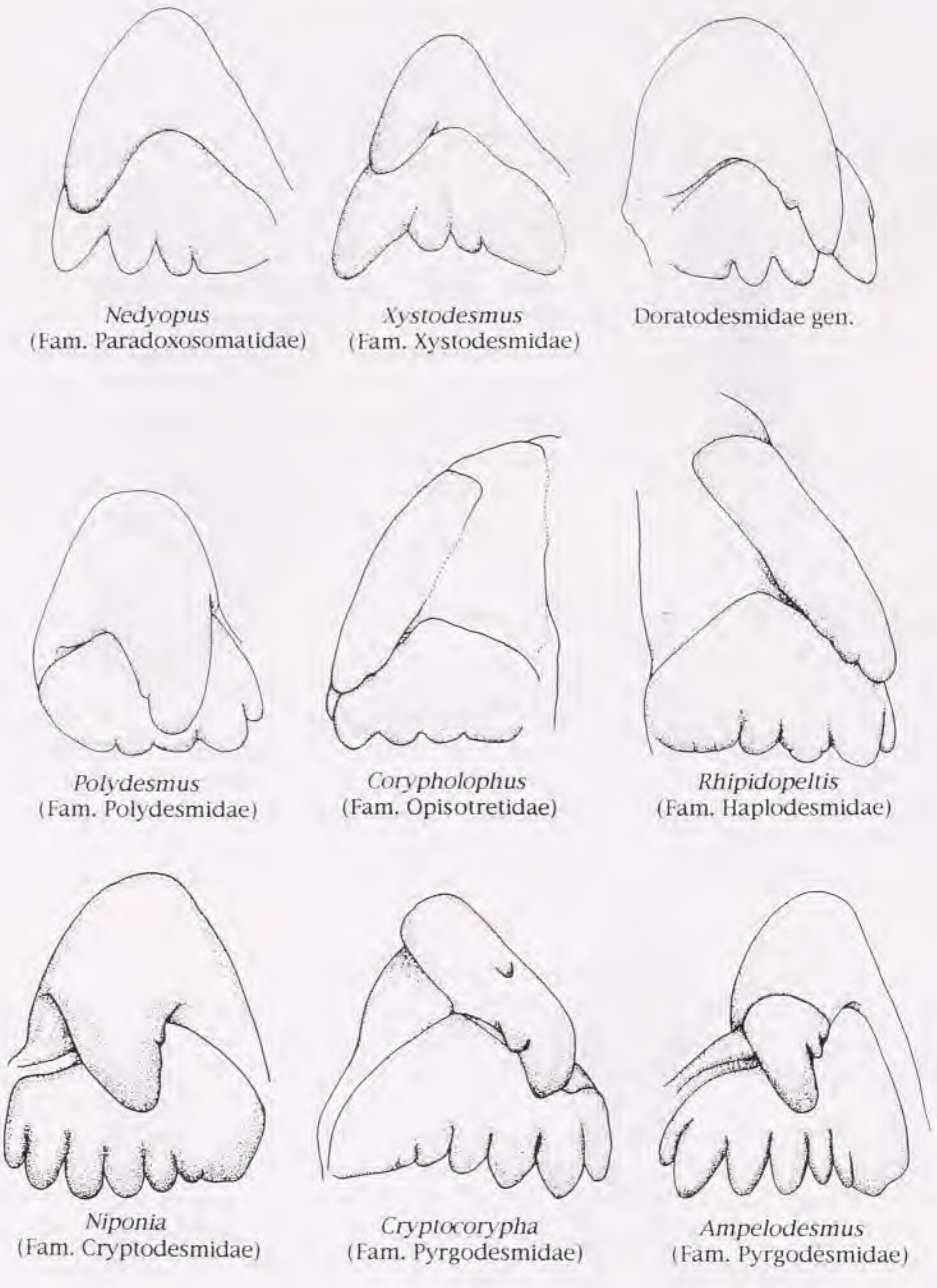


FIG. 2. — The external and internal teeth of the eight families in polydesmoid millipedes.

Fam. Paradoxosomatidae : Molar plate having wide sawtooth roof-like or lean-to roof-like molar process, lamellate fringe with sharp tine at apex without inner branches and thick molar tufts at proximal end (Fig. 3).

Fam. Xystodesmidae : Molar plate having shape sawtooth roof-like molar processes, lamellate fringe with slightly round tine at apex without inner branches and tiny molar tufts at proximal end (Fig. 4).

Source : MNHN, Paris

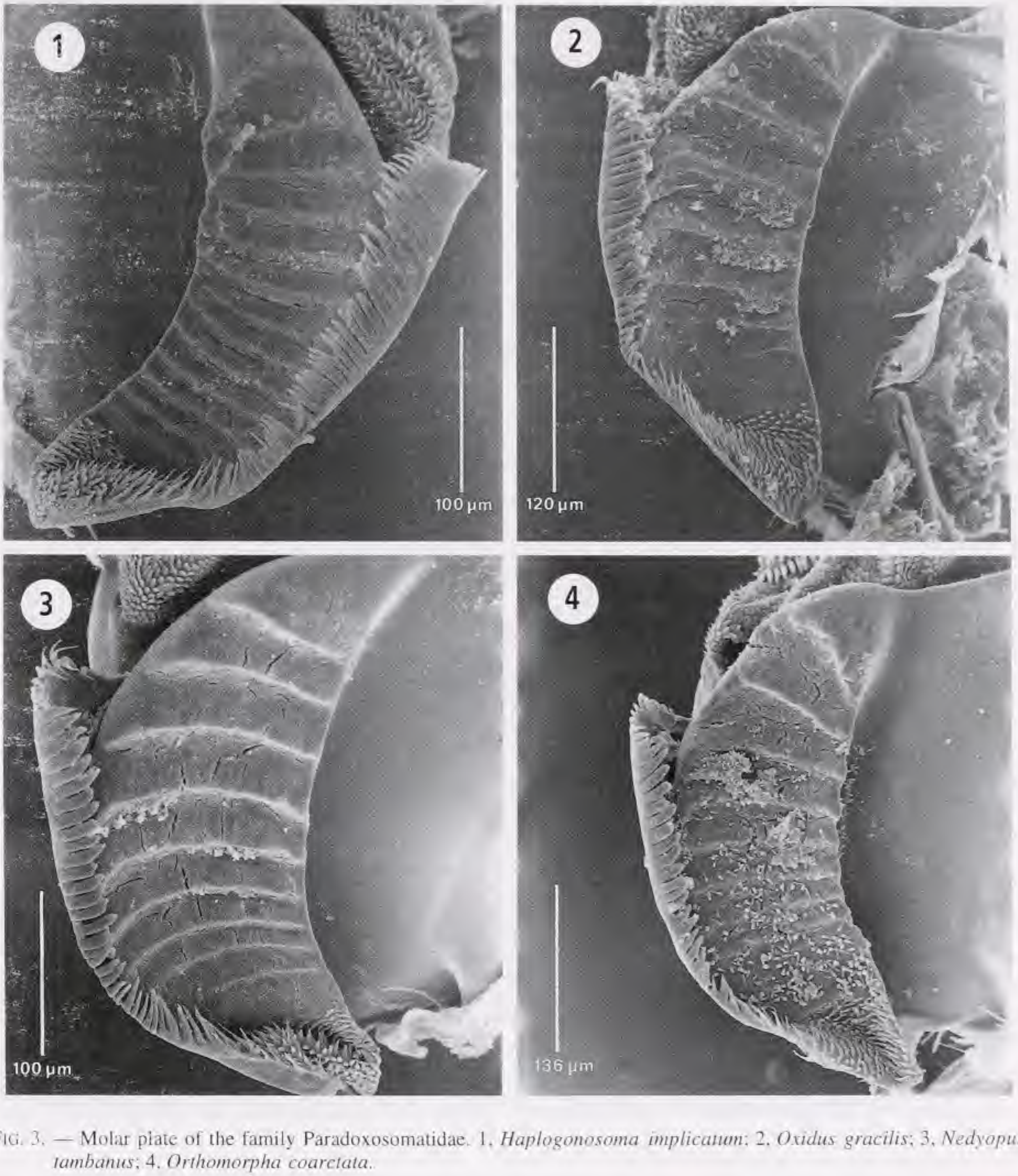


FIG. 3. — Molar plate of the family Paradoxosomatidae. 1, *Haplogonosoma implicatum*; 2, *Oxidus gracilis*; 3, *Nedyopus tambanus*; 4, *Orthomorpha coarctata*.

Source : MNHN, Paris

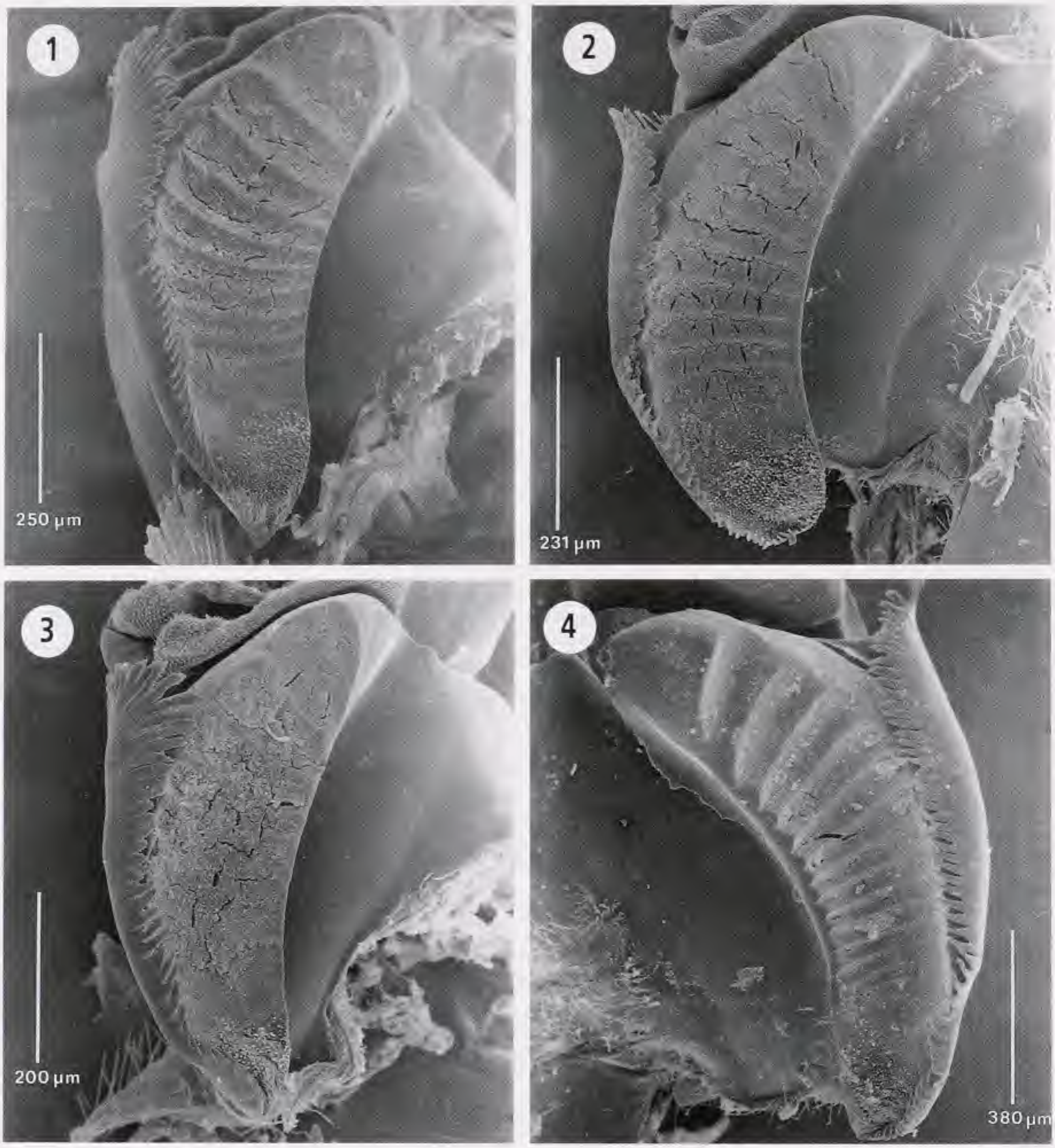


FIG. 4. — Molar plate of the family Xystodesmidae. 1, *Levizonus takakuwai*; 2, *Parafontaria laminata armigera*; 3, *Xystodesmus* sp.; 4, *Riukiaria* sp.

Fam. Polydesmidae : Molar plate having wide molar process, separated fringes with inner branches and thick, long molar tufts at the proximal end (Fig. 5).

Source : MNHN, Paris

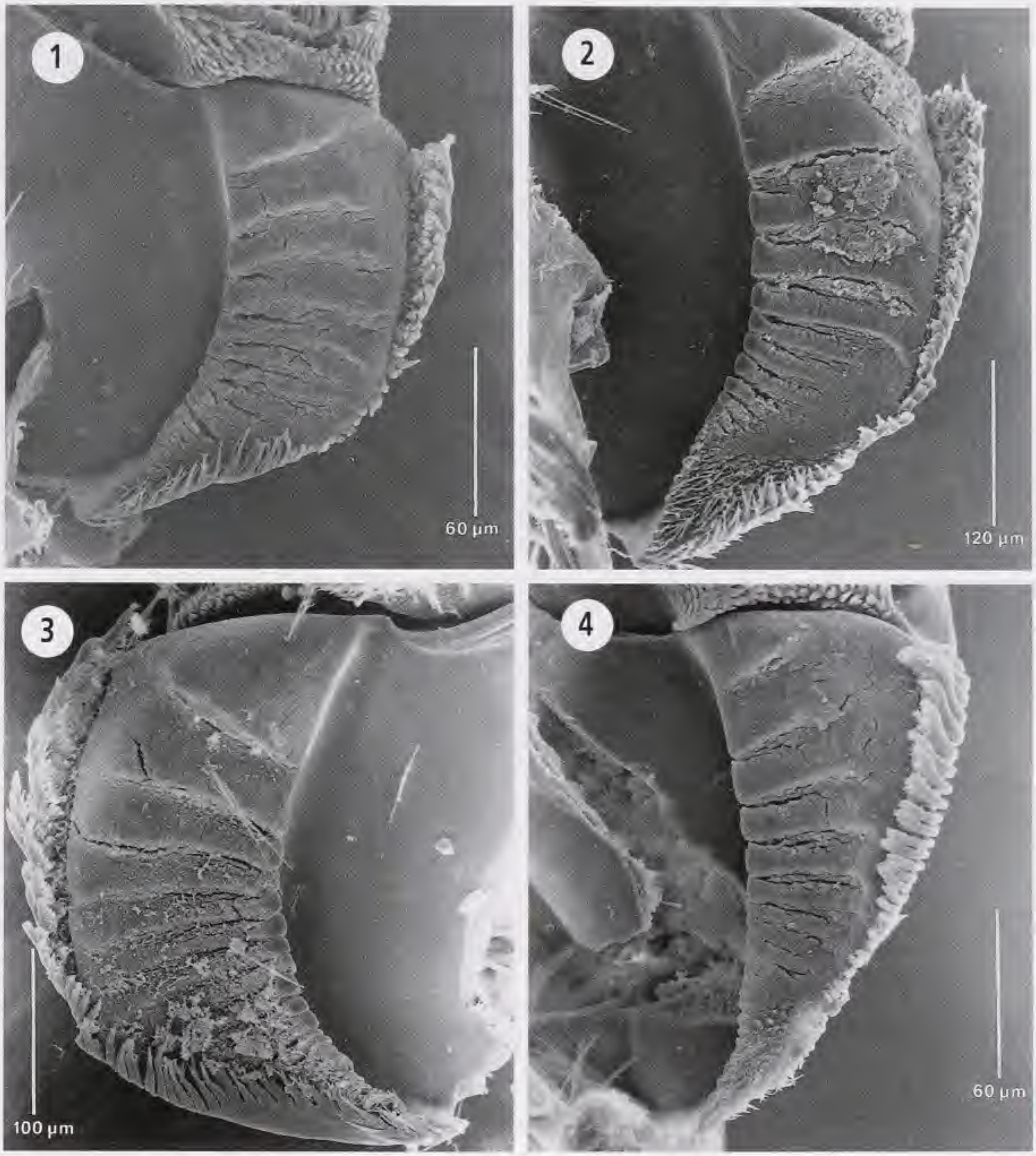


FIG. 5. — Molar plate of the family Polydesmidae. 1, *Polydesmus japonicus*; 2, *Epanerchodus mammillatus*; 3, *Prionomatis* sp.; 4, *Epanerchodus* sp.-1.

Source : MNHN, Paris

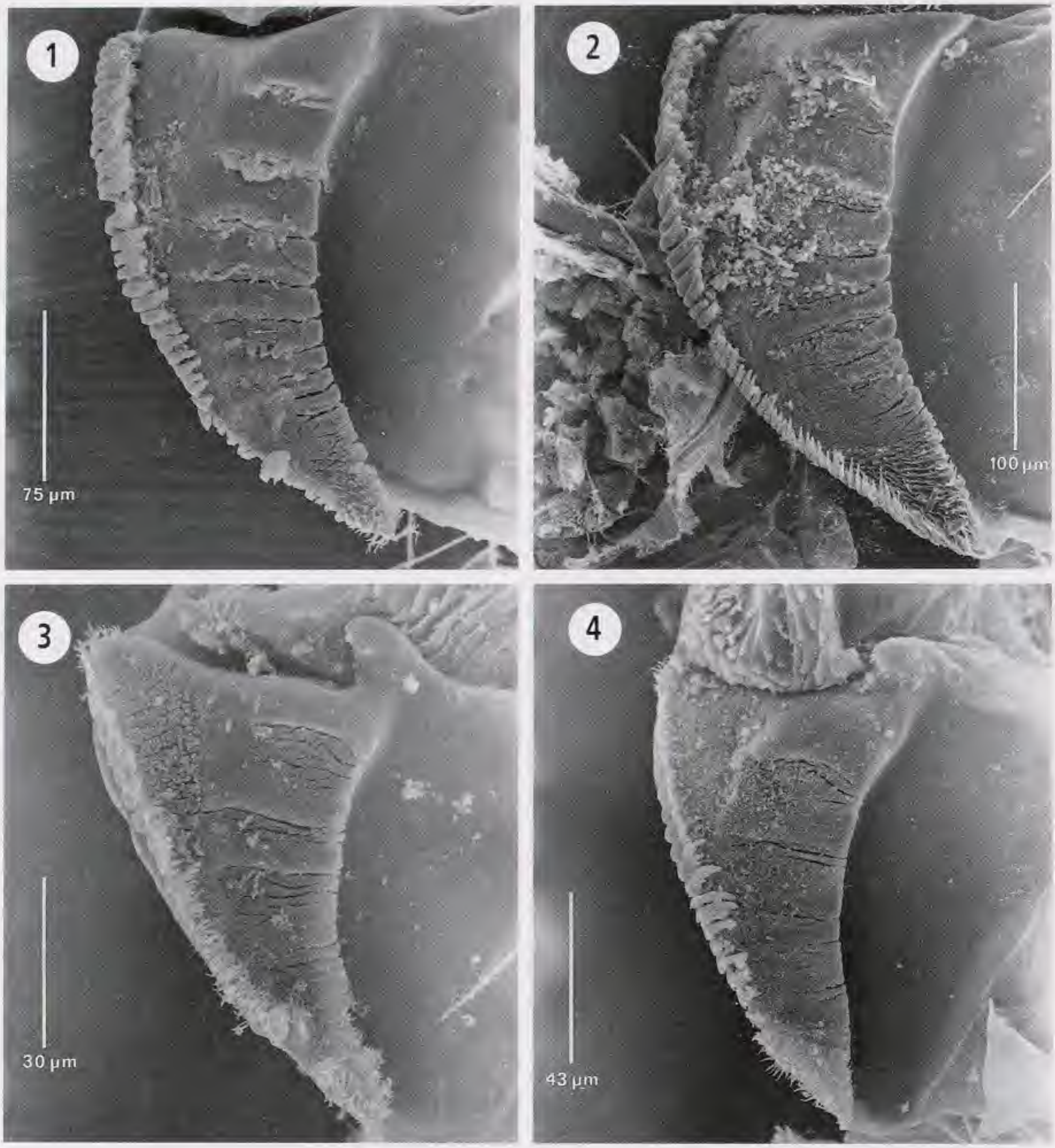


FIG. 6. — Molar plate of the families Cryptodesmidae and Pyrgodesmidae. Cryptodesmidae: 1, *Kiusiunum nodulosum*; 2, *Niponia nodulosa*. Pyrgodesmidae: 3, *Ampelodesmus granulosus*; 4, *Cryptocorypha japonica*.

Source : MNHN, Paris

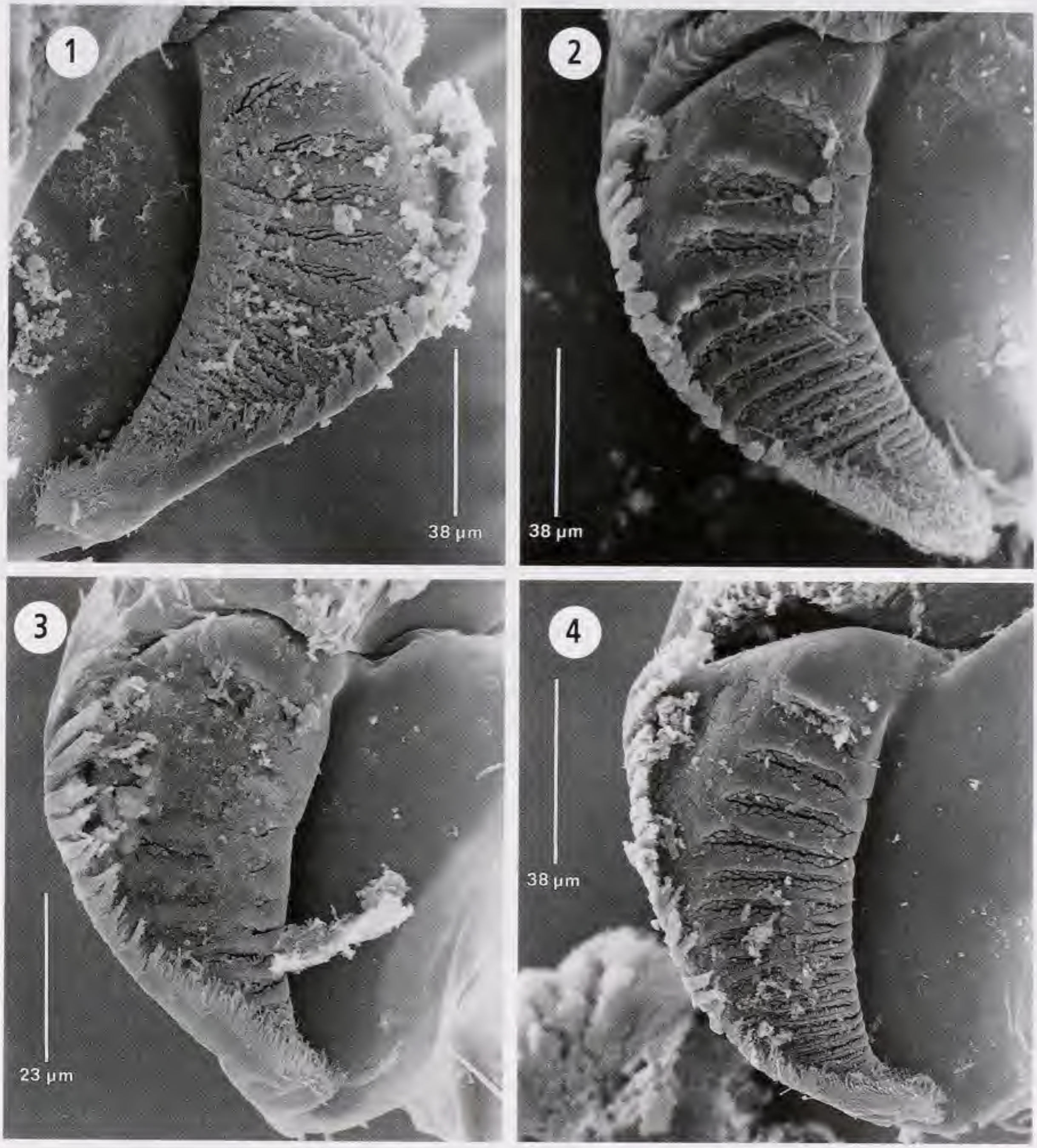


FIG. 7. — Molar plate of the family Doratodesmidae. 1, *Eucondylodesmus elegans*; 2, *Kylindogaster nodulosa*; 3, *Thelodesmus* sp.; 4, *Dimorphodesmus* sp.-1.

Source : MNHN, Paris

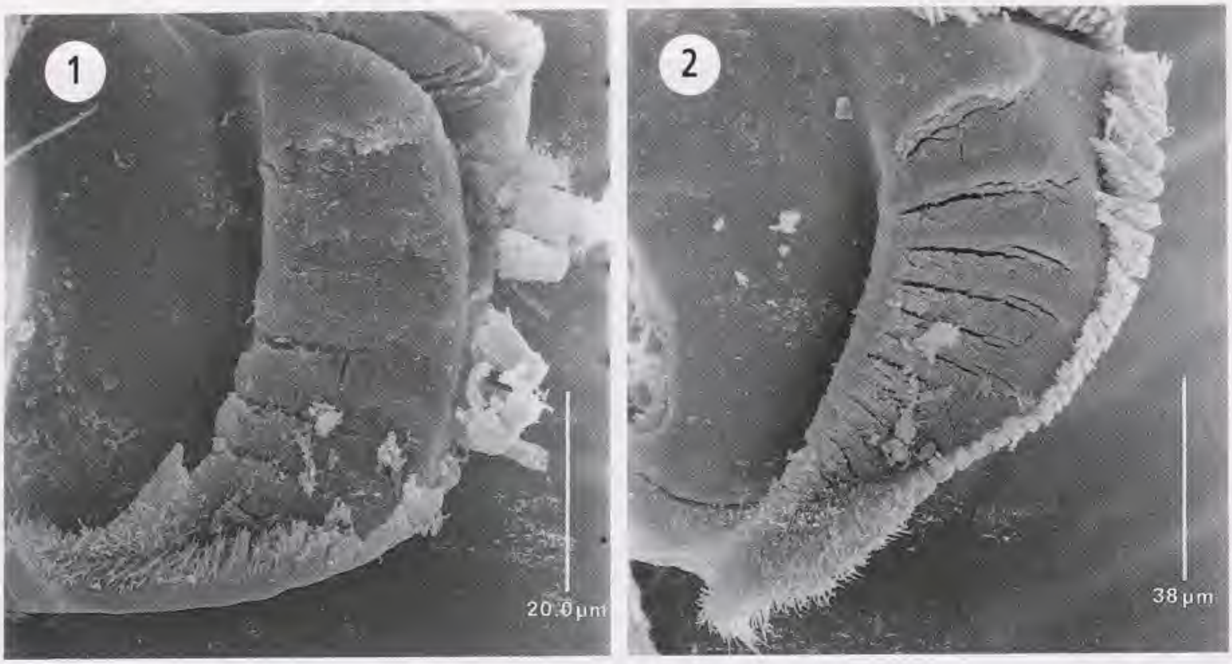


FIG. 8. — Molar plate of the families Opisotretidae and Haplodesmidae. Opisotretidae: 1, *Corypholophus* sp. Haplodesmidae: 2, *Rhipidopeltis* sp.

Fam. Opisotretidae : Molar plate having remarkably wide molar process, basal molar process with a stout denticle on ventral border, brushed fringes at apex with inner branches and long, numerous molar tufts (Fig. 8: 1).

Fam. Cryptodesmidae : Molar plate having wide molar process, wing process without granulated zone, branched fringes at apex with inner branches and slender molar tufts (Fig. 6: 1, 2).

Fam. Pyrgodesmidae : Molar plate having a molar hook, wide molar process, wing process with granulated zone, branched fringes at apex and slender molar tufts (Fig. 6: 3, 4).

Fam. Doratodesmidae : Molar plate internally having molar combs between narrow molar processes, branched fringes at apex with few inner branches and dense, molar tufts on a limited portion at proximal end (Fig. 7).

Fam. Haplodesmidae : Molar plate abruptly narrower sub-basally with dense molar tufts, branched fringes at apex with inner branches, and molar combs scarce or absent between molar processes (Fig. 8: 2).

KEY TO THE FAMILY OF THE POLYDESMOID MILLIPEDES BASED ON THE MOLAR

1. Molar plate with lamellate fringe-- 2
-. Molar plate with separate fringe--- 3
2. Molar plate with thick, long molar tufts---------------------------- Paradoxosomatidae
-. Molar plate with tiny, short molar tufts----------------------------- Xystodesmidae
3. Molar plate with molar wing process--------------------------------------- 4
-. Molar plate without molar wing process----------------------------------- 5

Source : MNHN, Paris

4. Molar plate with a molar hook-------------------------------------- Pyrgodesmidae
-. Molar plate without molar hook------------------------------------ Cryptodesmidae
5. Molar combs present between molar processes---------------------------- 6
-. Molar combs absent between molar processes----------------------------- 7
6. Molar combs abundant-- Doratodesmidae
-. Molar combs scarce or absent-------------------------------------- Haplodesmidae
7. Fringe narrow at apex--- Polydesmidae
-. Fringe brush-like at apex-- Opisotretidae

The following eleven genera well resemble morphologically each other: *Kiusiunum, Niponia, Cryptocorypha, Ampelodesmus, Pseudocatapyrgodesmus, Eucondylodesmus, Kylindogaster, Dimorphodesmus, Thelodesmus, Rhipidopeltis* and undetermined genus collected from China. These ten genera except the genus *Pseudocatapyrgodesmus* not investigated in this study were classified into four groups from intensive examinations on molar structure, and this grouping agreed with HOFFMAN (1980) as follows: Cryptodesmidae, *Kiusiunum* and *Niponia*; Pyrgodesmidae, *Cryptocorypha* and *Ampelodesmus*; Doratodesmidae, *Eucondylodesmus, Kylindogaster, Dimorphodesmus, Thelodesmus* and undetermined genus collected from China; Haplodesmidae, *Rhipidopeltis*. On the other hand, the genera *Prionomatis* and *Epanerchodus* of the family Polydesmidae is distinctly the same in molar structure (FIG. 5). Therefore the genus *Prionomatis* should be better considered as a synonym of the genus *Epanerchodus*.

As far as the present study is concerned, mandibular structures are fairly stable within taxa and distinctly different between taxa, clearly suggesting usefulness as an important diagnostic character in the taxonomy of the Polydesmoid millipedes.

REFERENCES

ATTEMS, C., 1937. — Myriapoda 3. Polydesmoidea. I. Fam. Strongylosomidae. *In* : F. E. SCHULZE, W. KÜKENTHAL & K. HEIDER, *Das Tierreich*, **68**, Berlin & Leipzig, W. de Gruyter & C° : 1-300.

ENGHOFF, H., 1979. — Taxonomic significance of the mandibles in the millipede Order Julida. *In* : M. CAMATINI, *Myriapod Biology*, London, Academic Press : 27-38.

ENGHOFF, H., 1981. — A cladistic analysis and classification of the millipede order Julida. *Z. zool. Syst. Evol.-Forsch.*, **19** : 285-319.

ENGHOFF, H., 1985. — Modified mouthparts in hydrophilous cave millipedes (Diplopoda). *Bijdragen tot de Dierkunde*, **55** : 67-77.

HOFFMAN, R. L., 1980. — *Classification of the Diplopoda*. Genève, Muséum d'Histoire Naturelle, (1979), 238 pp.

HOPKIN, S. P. & READ, H. J., 1992. — *The biology of millipedes*. Oxford, Oxford University Press, 233pp.

ISHII, K., 1988. — On the significance of the mandible as a diagnostic character in the taxonomy of penicillate diplopods (Diplopoda: Polyxenidae). *Can. Entomol.*, **120** : 955-963.

ISHII, K. & TAMURA, H., 1992. — The mandibular structure as a diagnostic character in taxonomy of diplopods. *Acta Zool. Fenn.*, **196** : 232-235.

LAUTERBACH, K. E., 1972. — Über die sogenannte Ganzbein-Mandibel der Tracheaten, insbesondere der Myriapoda. *Zool. Anz.* **188** : 145-154.

MANTON, S. M., 1964. — Mandibular mechanisms and the evolution of arthropods. *Philosophical Transactions of the Royal Society of London*, Series B, **247** : 1-183.

Source : MNHN, Paris

Source : MNHN, Paris

Systématique et biogéographie des diplopodes pénicillates des Îles Canaries et du Cap Vert

Monique NGUYEN DUY - JACQUEMIN

Muséum national d'Histoire naturelle, Laboratoire de Zoologie/Arthropodes
61, rue Buffon, F-75231 Paris, France

RÉSUMÉ

Quatre espèces de pénicillates ont été récoltées sur les îles Canaries et trois aux îles du Cap Vert. Trois de ces sept espèces sont nouvelles et font l'objet d'une description détaillée. Deux sont des Canaries : Fuertoventura, La Palma, Tenerife pour *Polyxenus oromii* n. sp. et Fuertoventura pour *Macroxenus enghoffi* n. sp. La troisième, *Anopsxenus caboverdus* n. sp., est de Santiago, l'une des îles du Cap Vert. Une forme incertaine de San Antão (Cap Vert) est nommée cf. *enghoffi*. Les trois autres espèces ont une répartition continentale ou insulaire plus ou moins étendue.

ABSTRACT

Systematic and biogeographical study of Diplopoda, Penicillata of Canary Islands and Cape Verde Islands.

Four species of Penicillata were collected from the Canary Islands and three from the Cape Verde Islands. These include three new species which are described in detail. Two of the new species are from the Canary Islands: *Polyxenus oromii* n. sp., from Fuertoventura and Tenerife; and *Macroxenus enghoffi* n. sp., from Fuertoventura; while the third, *Anopsxenus caboverdus* n. sp., is from Santiago, Cape Verde Islands. A form of uncertain status, referred to as *M.* cf. *enghoffi*, is recorded from San Antão (Cape Verde). The other three species collected have fairly widespread, continental or insular, distributions.

INTRODUCTION

Quatre espèces de pénicillates seulement ont été citées des îles de la Macaronésie : *Polyxenus lagurus* (L.) aux Açores (BRÖLEMANN, 1896 ; CONDÉ, 1961), *P. fasciculatus* Say, 1921 à Madère (CONDÉ & NGUYEN DUY - JACQUEMIN, 1994), *Lophoturus madecassus* (Marquet et Condé, 1950) et *Anopsxenus indicus* Condé et Jacquemin, 1963 aux îles du Cap Vert (ENGHOFF, 1993). L'examen des collections qui m'ont été confiées par les Dr. ENGHOFF, OROMI et VICENTE me permet d'exposer ici les premières données sur le peuplement des îles Canaries par les pénicillates et de compléter celui des îles du Cap Vert.

NGUYEN DUY - JACQUEMIN, M., 1996. — Systématique et biogéographie des diplopodes pénicillates des Iles Canaries et du Cap Vert. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 113-126. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

FAMILLE DES POLYXENIDAE

Polyxenus fasciculatus Say, 1921

STATIONS. — Gran Canaria. W of Artenara, 1200 m, slopes with *Adenocarpus* etc. under stones, n° 2707, 07.I.1990, H. ENGHOFF leg. : 1 mâle à 13 pp. (ad), 2 femelles à 13 pp. (ad.). — Cruz de Tejeda, 1500 m (27 km SW Las Palmas, loc. Luftlinie), wahrscheinlich Ziegenweide, sehr steinig, unter Steinen, Trocken bis wenig feucht, n° 4122, 24.IV.1976, W. HÜTHER leg. : 1 mâle à 13 pp. (ad.), 1 femelle à 13 pp (ad.), 2 femelles à 12 pp., 1 mâle à 12 pp.- Vega de Acusa, 15.XII.1987, R. RODRIGUEZ leg. : 1 mâle à 13 pp. (ad.). — Valle de Agaete, 30.X.1989, R. RODRIGUEZ leg. : 1 femelle à 13 pp (ad.).

Tenerife. Montaña de la Hoya, 6.XI.1989, R. RODRIGUEZ leg. : 1 femelle à 13 pp. (ad.). — Los Carboneros, 3.II.90, P. OROMI leg. : 2 mâles à 13 pp. (ad.), 1 ind. à 10 pp. — Vueltas Taganana, 19.I.1991, P. OROMI leg. : 2 mâles à 13 pp. (ad.), 3 femelles à 13 pp (ad.). — Agua Garcia et Las Mercedes, IV.94, M. BÂEZ leg. : 1 femelle à 13 pp. (ad.) et 1 femelle à 12 pp. — Sieste Cañadas, N.-E. du parc national de Las Cañadas, dans la litière de *Spartocytisus supranubius* et *Adenocarpus viscosus*, 10.VI.95, P. OROMI leg. : 8 femelles à 13 pp. (ad.), 2 mâles à 13 pp. (ad.), 2 mâles à 12 pp., 3 mâles à 10 pp., 1 femelle à 10 pp., 2 ind. à 8 pp.

Gomera. Barranco Nª Sª Guadaloupe, 550m, 23.XII.78, V. MONSERRAT leg. : 1 femelle à 13 pp. (ad.).

Hierro. Montaña de las Cuevas, 30.III.1989, R. RODRIGUEZ leg. : 1 femelle à 10 pp. — El Fayal c. 4 km SSW Mirador de Jinama, 1350 m, dense Fayal-Brezal, u. bark of log, 2.II.1989, A. et H. ENGHOFF leg. n° 242 : 2 mâles à 13 pp. (ad.), 1 mâle à 12 pp., 1 femelle à 12 pp., 1 ind. à 8 pp.

P. fasciculatus est très répandu dans le Centre et le Sud-Est des Etats-Unis, où il remplace la forme unisexuée de *P. lagurus* (CONDÉ & NGUYEN DUY - JACQUEMIN, 1994), aux Bermudes (CONDÉ, 1972) et à Madère (CONDÉ, 1961, sous le nom de *P. lagurus*, forme bisexuée). Il est très voisin de la forme bisexuée de *Polyxenus lagurus*, très commune en Europe, notamment sur le pourtour de la Méditerranée, et présente aux Açores ; il ne s'en distingue que par un nombre plus grand de sensilles basiconiques sur le 6ème article antennaire et un nombre inférieur de sensilles sur l'expansion latérale des palpes gnathochilariaux (NGUYEN DUY - JACQUEMIN, 1976).

FIGS. 1-6. — *Polyxenus oromii* n. sp. : ♀ paratype de La Palma, 1 = tête, face dorsale, 2 = palpe droit du gnathochilarium, 3 = antenne gauche ; autres ♀ adultes de La Palma, 4 et 5 = sensilles des articles VI et VII d'une antenne gauche, 6 = griffe et épine tarsale d'une patte IX gauche.

FIG. 1-6. — Polyxenus oromii *n. sp. : ♀ La Palma paratype, 1 = head, dorsal side, 2 = right palp of the gnathochilarium, 3 = left antenna; other adults ♀ of La Palma, 4 and 5 = sensillae of left antennal articles VI and VII, 6 = claw and tarsal spine of a left leg IX.*

FIGS. 7 à 9. — *Polyxenus chalcidicus* Condé et Nguyen, 1971 (d'après les auteurs : p. 1254) : 7 et 8 = sensilles de l' article VI d'un ♂ à 12 pp et de l'article VII du ♂ holotype de l'île d'Eubée, 9 = Griffe de la patte III droite du ♂ holotype.

FIG. 7 à 9.— Polyxenus chalcidicus *Condé et Nguyen, 1971 (after the authors: p. 1254): 7 and 8 = sensillae of article VI of a ♂ with 12 pairs of legs and article VII of the holotype ♂ from Eubea Island, 9 = claw of right leg III of holotype ♂.*

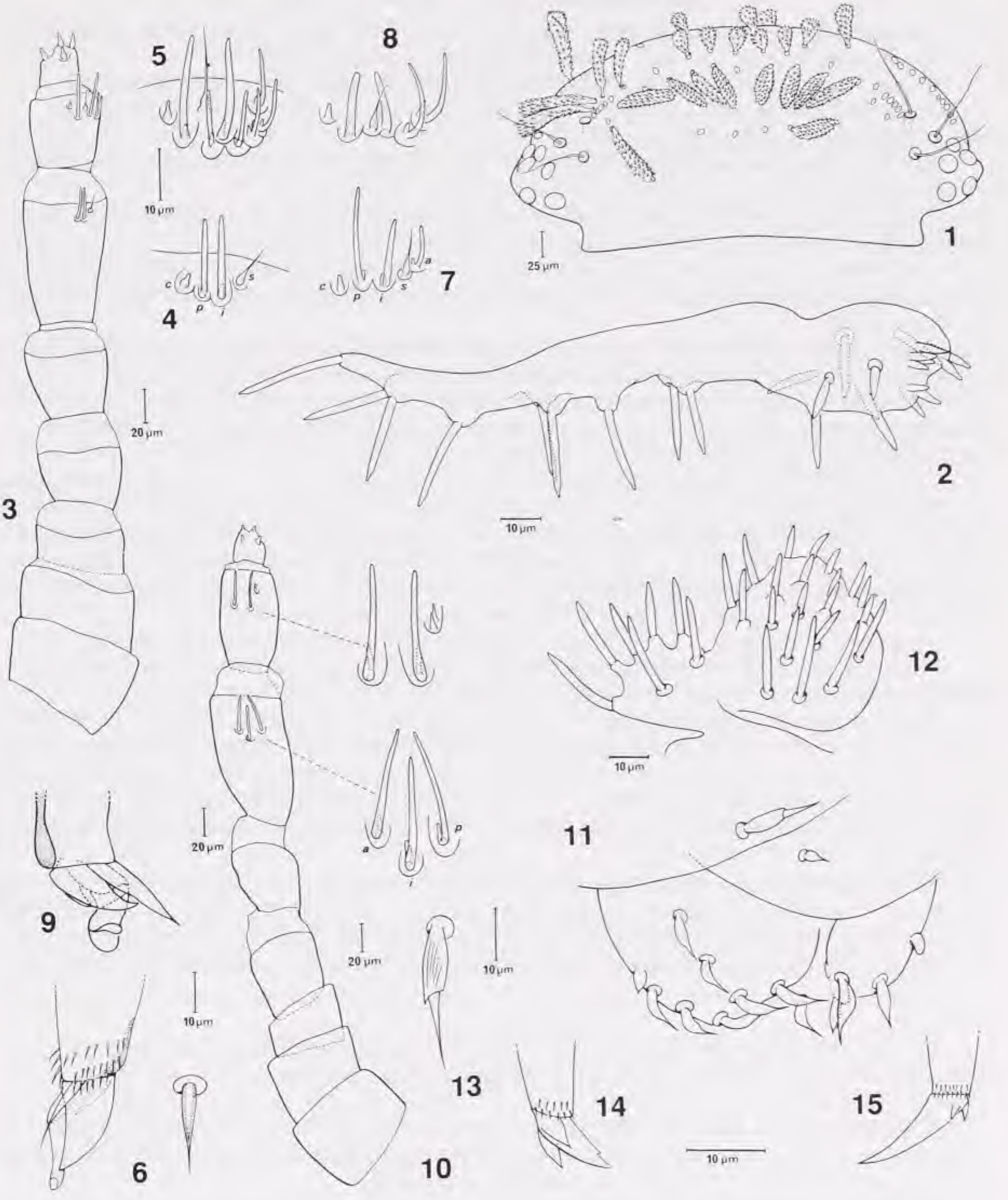
FIGS. 10 à 14. — *Anopsxenus caboverdus* n. sp. : ♀ paratype de Santiago, 10 = antenne droite avec détail des sensilles des articles VI et VII, 11 = vulve gauche ; ♀ holotype de Santiago, 12 = palpe gauche du gnathochilarium, 13 et 14 = soie du subcoxa et griffe de la patte IV gauche.

FIG. 10 à 14. — Anopsxenus caboverdus *n. sp.: paratype ♀ of Santiago, 10 = right antenna with detailed sensillae of articles VI et VII, 11 = left vulva; holotype ♀ of Santiago, 12 = left palp of the gnathochilarium, 13 and 14 = subcoxa seta and claw of the left leg IV.*

FIG. 15. — *Anopsxenus indicus* : ♀ adulte, griffe de la patte VI gauche.

FIG. 15. — Anopsxenus indicus *: adult ♀ , claw of the left leg VI.*

Source : MNHN, Paris



Abréviations. Sensilles : basiconique antérieur (*a*) ; cœloconique (*c*) ; basiconique intermédiaire (*i*) ; basiconique postérieur (*p*) ; sétiforme antérieur (*s*).

Abbreviations. Sensillae: anterior basiconicum (a); cœloconicum (c); intermediate basiconicum (i); posterior basiconicum (p); anterior setiform (s).

Source : MNHN, Paris

Polyxenus oromii n. sp. (Figs. 1-6)

STATION. — La Palma. Teneguia Colada Costera, n° 5753, P. OROMI leg. : 2 mâles à 13 pp. (ad.), 7 femelles à 13 pp. (ad.), 1 femelle à 12 pp., 1 mâle à 10 pp.

Tenerife. Punta del Teno, n° 5760, 6-10. IV. 1988, P. OROMI leg. : 1 mâle à 12 pp.

Fuertoventura. Puerto Lajas, zone supralittorale, 13. IV.1987, R. RODRIGUEZ leg. : un mâle à 12 pp., une femelle à 12 pp.

Les spécimens de La Palma et Tenerife ont tous été récoltés sur des laves récentes, en bordure de mer.

DESCRIPTION. — Un mâle (holotype) et une femelle (paratype) adultes de La Palma, montés dans le médium II de Marc André ont servi pour la description.

Longueurs.- Corps (sans le pinceau caudal) : holotype = 1,50 mm ; paratype = 1,80 mm. Pinceau caudal : holotype = 0,20 mm. 2ème tarse de la 13ème paire de pattes : holotype = 80 µm ; paratype = 82 µm.

Tête.- Plages postérieures du vertex coalescentes sur la ligne médiane, comprenant deux rangées de trichomes, l'antérieure d'une vingtaine de ces phanères, la postérieure de 10 à 13. En arrière de ces rangées, quelques trichomes médiaux : 3, un antérieur et deux postérieurs, disposés en triangle chez l'holotype et 4 sur une seule rangée chez le paratype. L'orientation et la taille de ces trichomes sont indiquées sur la Fig. 1.

Le 6ème article antennaire (Fig. 3), une fois 1/3 à une fois 1/2 plus long que large, porte 2 sensilles basiconiques épais, un sensille sétiforme antérieur et un sensille cœloconique postérieur; le basiconique (*i*) proche du sétiforme (*s*) est plus long et à peine plus épais que le postérieur (*p*) (Fig. 4). Le 7ème article porte toujours 2 sensilles basiconiques épais, séparés par un sensille sétiforme à base plus distale, et suivis par un sensille cœloconique postérieur ; 3 à 5 sensilles basiconiques grêles entourent le basiconique épais antérieur (Fig. 5).

6 stemmates subégaux : 5 tergaux et un sternal antérieur. Trichobothries typiques.

Labre couvert de petits tubercules acuminés, ceux des rangées antérieures ne paraissant pas plus volumineux que les autres ; 4+4 lamelles marginales.

Palpes du gnathochilarium avec 17 sensilles sur le mamelon ; bras latéraux environ deux fois plus longs que le plus grand diamètre du mamelon, portant 9 sensilles chez les deux sexes.

Tronc.- Collum avec 3 rangées de trichomes ; la rangée intermédiaire comprenant chez le mâle 8 trichomes subsphériques, dirigés vers l'avant. Tergites II à VIII avec 44 à 55 trichomes sur deux rangées subrectilignes réunies latéralement par quelques phanères formant l'ébauche d'une rosette.

Soies biarticulées des pattes, réparties ainsi chez le ♂ holotype : 2 sur les subcoxas I et II uniquement ; 1 sur tous les coxas et trochanters ; 1 sur les tibias I à XII. Épine du 2ème tarse très effilée, de longueur à peine inférieure à la griffe ; processus antérieur du télotarse très fin et plus court que la griffe, processus postérieur lamellaire assez étroit et denticule basal effilé (Fig. 6).

Mâle. Subcoxas VIII et IX dépourvus d'invaginations glandulaires. Pénis sans zone glabre.

Telson.- De même type que celui de *P. lagurus*. Le groupe médio-dorsal avec environ 23 trichomes barbelés chez la femelle. Trichomes appendiculés, pourvus de 3 ou 4 expansions sous la crosse terminale.

AFFINITÉS. — La nouvelle espèce *P. oromii* est proche de *P. chalcidicus* par les trichomes de la tête et des tergites troncaux présentant la même forme et la même distribution, mais elle s'en distingue par un ensemble de caractères énumérés ci-dessous :

- sensilles des articles antennaires VI et VII : l'article VI ne porte que 2 sensilles basiconiques, au lieu de 3, l'antérieur faisant défaut (Fig. 7) ; sur l'article VII, le nombre de sensilles basiconiques grêles est plus élevé (4 à 7 au lieu de 2 : Fig. 8) ;

Source : MNHN, Paris

- bras latéraux des palpes du gnathochilarium : 9 sensilles au lieu de 12. La femelle adulte de Lahav (Israël), rapportée à *P. chalcidicus* avec quelques réserves, ne possède aussi que 9 sensilles (CONDÉ & NGUYEN DUY - JACQUEMIN, 1971) ;

- processus antérieur du télotarse beaucoup moins développé ;

- mâles dépourvus de glandes subcoxales qui tissent les fils signalisateurs des spermatophores. Les mâles de *P. chalcidicus* sont déjà dépourvus de ces formations à la base des pattes IX, tandis que les autres espèces de *Polyxenus* en possèdent aux pattes VIII et IX.

Le moindre nombre de sensilles aux palpes du gnathochilarium, constaté chez *P. oromii*, peut être considéré comme une persistance, chez cette espèce, de la formule des stades juvéniles II, III et IV de *P. chalcidicus* porteurs de 9 sensilles ; de même, l'absence du sensille basiconique antérieur de l'article antennaire VI, commune aux deux premiers stades larvaires de *P. chalcidicus* ; et celle enfin des glandes subcoxales VIII apparaissant ordinairement au stade VI.

DISCUSSION. — Le genre *Polyxenus* compte à présent 4 espèces nominales possédant des trichomes tergaux globuleux : *P. lapidicola* Silvestri, *in* BERLESE, 1903 ; *P. macedonicus* Verhoeff, 1952 ; *P. chalcidicus* Condé et Nguyen Duy - Jacquemin 1971 et *P. oromii n.* sp.

Les types de *P. lapidicola* ont été récoltés dans des fissures de rochers sur le rivage marin, près de Portici, dans une zone mouillée par mer agitée. L'espèce a été ainsi considérée comme halophile (ou halobie), d'autant qu'elle a été recherchée sans succès dans des biotopes secs, sur les pentes du Vésuve en particulier (SILVESTRI, 1903). La description est très incomplète, comme le souligne VERHOEFF (1921) qui citera l'espèce de Macédoine (Skoplje) (1941) et de l'île d'Ischia (1952). CONDÉ (1950, 1953) signale *lapidicola* de Saint-Raphaël, puis de Corse, plus ou moins loin de la mer, mais jamais sur le rivage. Tout récemment enfin, ENGHOFF & SCHEMBRI (1989) attribuent à *lapidicola* des spécimens de Malte, récoltés dans la litière, sous d'épais buissons, sans justifier cette détermination.

L'examen de 3 syntypes de *P. macedonicus*, de Skoplje, conservés dans la collection K. Verhoeff, à Munich, a permis de décrire les groupes de sensilles des articles VI et VII de l'antenne avec, pour conséquence, l'attribution à *P. macedonicus* des spécimens de France méridionale et de Corse rapportés à *P. lapidicola* (CONDÉ & NGUYEN DUY - JACQUEMIN, 1971 : 1256).

P. chalcidicus est largement répandu en Grèce continentale : Thessalie, Béotie, Attique (collections du Muséum d'Histoire naturelle de Genève, CONDÉ det., inédit) ; la présence de 12 sensilles, à partir du stade à 8 pp., sur les expansions latérales des palpes du gnathochilarium est ainsi confirmée, de même que celle d'invaginations glandulaires sur les subcoxas VIII des mâles, à partir du stade à 10 pp.

P. oromii, enfin, a été récolté dans des biotopes littoraux, semblables à ceux qui ont livré les types de *P. lapidicola*. Cette dernière espèce demeurera énigmatique jusqu'à la révision des types.

Macroxenus enghoffi n. sp. (Figs. 16-26)

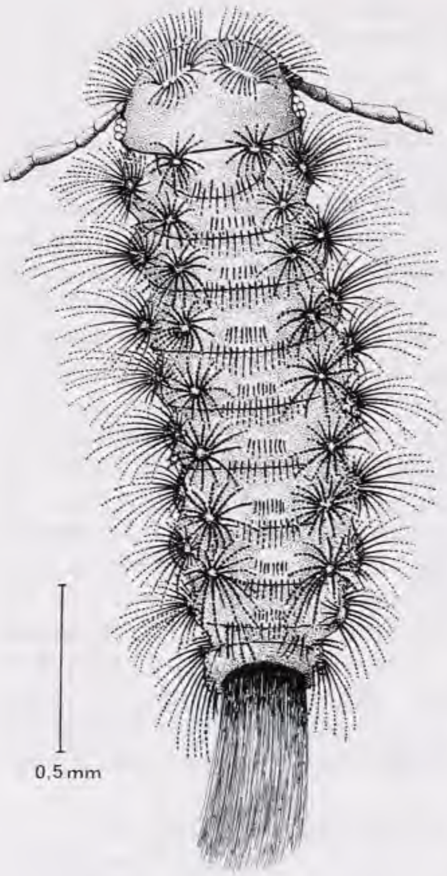
STATION. — Fuertoventura. Cumbre Jandia, 14.II.1977, P. OROMI leg. : 4 mâles à 13 pp. (ad.), 3 femelles à 13 pp. (ad.), 2 mâles à 12 pp., 1 mâle à 10 pp.

DESCRIPTION. — 2 mâles adultes, 1 femelle adulte, le mâle à 10 pp., montés dans le médium II de Marc André, constituent la série typique.

Adultes.

Longueurs.- Corps (sans le pinceau caudal) : mâles = 3,30 mm (holotype) et 3 mm ; femelle = 4 mm. Pinceau caudal = 0,40 mm (holotype). Trichomes du vertex = 0,20 mm (holotype). 2ème tarse de la 13ème paire de pattes : mâles = 172 µm (holotype) et 179 µm ; femelle = 188 µm.

Source : MNHN, Paris



Tête.- Plages postérieures du vertex allongées transversalement et très fortement obliques, plus de deux fois et demi plus longues que leur écartement. Elles comprennent chacune 29 trichomes chez l'holotype et 24 chez la femelle formant une rangée antérieure de 13 à 18 trichomes rapprochés les uns des autres et une rangée postérieure de 8 à 10 trichomes plus espacés que les précédents, le plus latéral étant nettement plus éloigné des autres (Fig. 18) ; parfois une 3ème rangée très courte de 2 à 4 trichomes s'ajoute entre les deux autres, vers la région centrale de la tête.

Les longueurs relatives des articles antennaires sont données par la Figure 17. Article VI deux fois plus long que large portant 13 (holotype et femelle) à 16 sensilles basiconiques subégaux, très effilés à l'apex, insérés sur une surface triangulaire dont une base suit la limite distale de l'article ; à ceux-ci s'ajoutent un sensille cœloconique postérieur (*c*) et un sensille sétiforme antérieur. L'article VII porte toujours deux sensilles basiconiques subégaux, séparés par un sensille sétiforme et accompagnés d'un sensille cœloconique postérieur.

Trichobothries subégales, à funicule grêle. 8 stemmates : 6 dorsaux, un latéral et un ventral (Fig. 18).

FIG. 16. — Mâle adulte de *Macroxenus enghoffi* n. sp, habitus, face dorsale.

FIG. 16. — Adult male of Macroxenus enghoffi *n. sp, habitus, dorsal view.*

Marge antérieure du labre bordée de 15 (♀) à 22 (holotype, Fig. 20) lamelles arrondies, aussi hautes que larges, sauf aux extrémités latérales. Face externe couverte de granules pourvus d'une petite pointe apicale ; les plus marginaux, sur 1 à 3 rangs, sont plus volumineux, les suivants diminuent progressivement de taille jusqu'à la moitié de la largeur du labre. 10 (holotype) à 13 soies grêles bordent la limite clypéale, elles sont presque deux fois plus courtes que la plus grande largeur du labre.

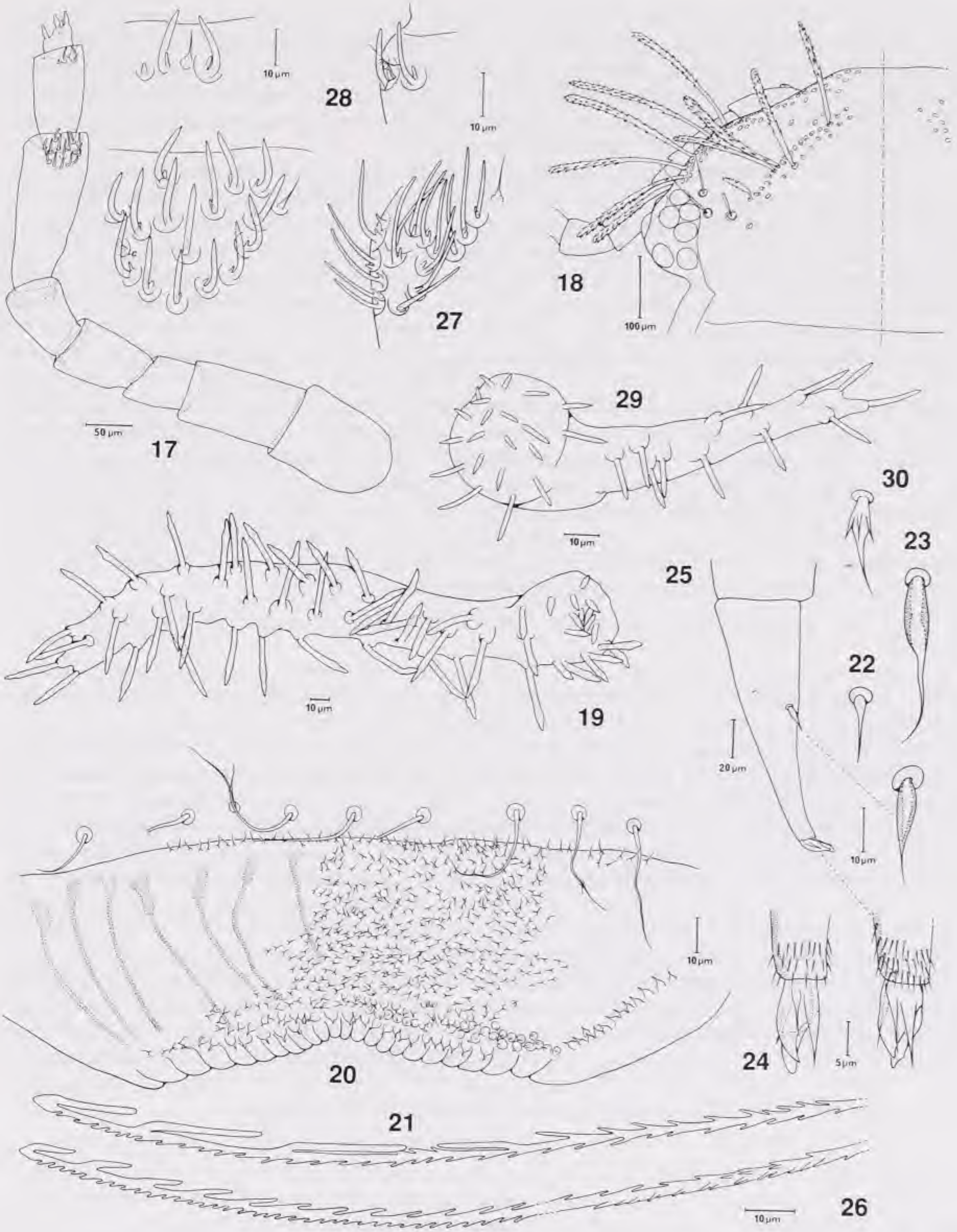
FIGS. 17-26. — *Macroxenus enghoffi* n. sp. : ♂ holotype de Fuertoventura, 17 = antenne gauche, face dorsale, avec détail des sensilles des articles VI et VII, 18 = demi-tête gauche, face dorsale, 19 = palpe droit du gnathochilarium, 20 = labre (une partie seulement des granules est dessinée), 21 = trichome hamulé du telson, 22 = soie du tibia de la patte I gauche, 23 = soie du subcoxa de la patte III gauche, 24 = griffe de la patte X droite ; ♀ adulte n°2, 25 = tarse de la patte I droite avec détail de l'épine et de la griffe, 26 = trichome à crochets spécifique des ♀.

FIG. 17-26. — Macroxenus enghoffi *n. sp.: holotype ♂ of Fuertoventura, 17 = left antenna, dorsal side, with detailed sensillae of articles VI et VII, 18 = half left head, dorsal side, 19 = right palp of the gnathochilarium, 20 = labrum (only a part of the granules is drawn), 21 = trichome with hooks of the telson, 22 = tibial seta on left leg I, 23 = subcoxal seta on left leg III, 24 = claw of the right leg X; adult ♀ n°2, 25 = tarsus of the right leg I with detailed spine and claw, 26 = trichome ♀ - specific hooks.*

FIGS. 27 à 30. — *Macroxenus* cf. *enghoffi* : ind. à 8pp de S. Antão, 27 et 28 = sensilles des articles VI et VII de l'antenne gauche, 29 = palpe gauche du gnathochilarium, 30 = soie du subcoxa de la patte I gauche.

FIG. 27 à 30. — Macroxenus *cf.* enghoffi *: ind. (8 pairs of legs) of S. Antão, 27 and 28 = sensillae of left antennal articles VI et VII, 29 = left palp of the gnathochilarium, 30 = subcoxal seta of the left leg I.*

Source : MNHN, Paris



Source : MNHN, Paris

Palpes du gnathochilarium à expansion latérale environ 4 fois plus longue que le plus grand diamètre du mamelon, portant 34 et 37 sensilles chez l'holotype (Fig. 19), 43 et 44 sensilles chez l'autre mâle et 15 sensilles chez une femelle[1]. Tous ces sensilles présentent une pseudoarticulation à peu de distance de l'apex. Le mamelon des mâles porte 18 à 20 sensilles et celui de la femelle 20 et 21 sensilles, de longueurs inégales, mais pseudoarticulés comme ceux de l'expansion, à l'exception des 7 antéro-internes courts.

Tronc.- Les plages latérales des tergites (collum et tergites IX-X exceptés) sont 2 à 3 fois plus courtes que leur écartement. Elles portent de 43 à 65 trichomes (♂), 33 à 49 (♀) et sont réunies entre elles par une rangée marginale postérieure sinueuse de 14 à 21 trichomes au collum, 26 à 48 (♂) et 23 à 35 (♀) aux tergites II à VIII ; en avant de la rangée marginale 5 à 14 trichomes non alignés sont présents sur les tergites II à X de l'holotype, II à IX des 2 autres spécimens et 2 sont présents uniquement sur le collum de l'holotype. Tous ces trichomes sont orientés vers l'arrière.

Soies des subcoxas (Fig. 23), coxas et trochanters à funicule fusiforme glabre ; il y en a une seule au subcoxa I, deux ou trois aux subcoxas II à XIII des ♂ et II à XII de la ♀ ; une seule au bord distal de chaque coxa et trochanter. Deux soies (parfois 1 ou 3) de même type, mais beaucoup plus petites, se rencontrent sur la région moyenne des trochanters ; une seule au bord distal des fémurs des pattes II à XIII des ♂, II à XII de la ♀ et au bord distal de chaque tibia (Fig. 22). L'épine du 2ème article des tarses est prolongée par une pointe extrêmement fine qui souvent n'apparaît pas au microscope ; sa longueur est voisine ou légèrement supérieure (1,1 à 1,2 fois) à celle de la griffe de la patte correspondante (Fig. 25). Griffe courte et trapue, pourvue de deux dents accessoires (antérieure et postérieure) subégales, longues et effilées (Figs. 24, 25). Processus télotarsaux sétiforme et lamellaire présents.

♂. Penis sans zone pyriforme glabre. Vastes invaginations glandulaires sur les subcoxas VIII et IX.

Telson.- Il appartient au type II, basé sur le genre *Macroxenus* , et défini par CONDÉ (1970) ; de chaque côté, 10 à 13 grosses embases de trichomes barbelés (*c*), groupées en une plage subcirculaire, occupent une échancrure de la marge antérieure du pinceau ; au bord antéro-interne de la plage, l'embase de *b* se distingue des autres par sa paroi un peu plus mince et sa forme plus allongée ; un seul trichome *a* en avant de chaque pinceau. Trichomes hamulés du pinceau caudal portant généralement 3 crosses (Fig. 21), parfois 4. En plus des trichomes barbelés et hamulés des mâles, les femelles possèdent un type différent de trichomes hamulés (Fig. 26). La hampe de ces trichomes est garnie, vers l'apex, d'une rangée rectiligne de crochets à pointe orientée vers la base du poil, de taille décroissant rapidement jusqu'à devenir de petites dents sur plus de la moitié de la longueur du phanère ; ces dents sont ensuite remplacées par des dents d'orientation inverse, c'est à dire dirigées vers l'apex, comme c'est le cas pour tous les trichomes. Ces poils caudaux, spécifiques des femelles, paraissent occuper une position ventrale, mais leur emplacement est impossible à reconnaître d'après la structure de leur cupule d'insertion ne pouvant être distinguée de celle des autres trichomes hamulés. C'est la seconde fois qu'un caractère sexuel secondaire concernant la structure d'un type de poil du pinceau caudal est observé chez un pénicillate. La première fois (CONDÉ & NGUYEN DUY - JACQUEMIN, 1990), il s'agissait du mâle du polyxénidé *Unixenus* aff. *broelemanni* (Condé & Jacquemin, 1963), qui est dépourvu des trichomes hamulés présents chez la femelle.

---

1. Chez *Macroxenus rubromarginatus*, les palpes du gnathochilarium des mâles et des femelles portent le même nombre de sensilles (24-26) sur l'expansion latérale, mais chez *M. caingangensis*, il y en a 16 au plus chez les femelles et 18 à 28 chez les mâles (CONDÉ & MASSOUD, 1974).

Source : MNHN, Paris

Immature.

♂ à 10 pp.

Les articles antennaires VI portent 12 et 13 sensilles basiconiques grêles ; les palpes du gnathochilarium ont chacun 20 sensilles sur le mamelon et respectivement 17 et 19 sensilles sur l'expansion latérale. Marge antérieure du labre bordée par 5+6 lamelles hyalines latérales. Une invagination glandulaire sur le subcoxa VIII. Pas de bourgeons externes ; faisceaux transitoires présents.

Plage subcirculaire de 6 et 7 trichomes *c* ; 3 trichomes *a* sur le telson.

AFFINITÉS. — Les deux espèces de *Macroxenus* décrites jusqu'ici, *M. rubromarginatus* (Lucas, 1846), d'Afrique septentrionale, et *M. caingangensis* (Schubart, 1944), du Brésil, sont excessivement voisines l'une de l'autre (CONDÉ, 1971 : 633). Les sensilles basiconiques de l'article VI sont disposés en une rangée transverse, rectiligne, de 5 et parfois 6 unités, avec un sensille cœloconique situé avant les 2 basiconiques postérieurs, soit 3+cœl.+2 ou 4+cœl.+2. Les nombreux sensilles de l'article VI de *M. enghoffi*, disposés en un groupe subtriangulaire, évoquent davantage *Macroxenodes bartschi* (Chamberlin, 1922), redécrit assez récemment (NGUYEN DUY - JACQUEMIN & CONDÉ, 1984).

Les espèces à sensilles gnathochilariaux pseudoarticulés, réparties entre les genres *Macroxenus* Brölemann, 1917, *Macroxenodes* Silvestri, 1948 et *Chilexenus* Silvestri, 1948 ont en commun un telson du type II qui est unique dans le groupe - de même que les sensilles pseudoarticulés - et constitue un argument de parenté indiscutable. Toutefois, la définition de ces trois genres est peu satisfaisante et, dans l'attente d'une révision des types, l'attribution générique des espèces doit être considérée comme provisoire.

Macroxenus cf. ***enghoffi*** (Figs 27-30)

STATION. — S. Antão. Around villa de Ribeira Grande, 4-7.XII.1988, A. VAN HARTEN leg. : 1 ind. à 8 pp.

DESCRIPTION.

Longueurs.- Corps (sans pinceau caudal) = 1,70mm. 2e tarse de la VIIIe paire de pattes = 99 µm.

Tête.- Plages postérieures du vertex composées de 10 trichomes : 7 à la rangée antérieure, 3 à la rangée postérieure. 15 et 16 sensilles basiconiques grêles (Fig. 27) sur le 6ème article antennaire ; 20 et 21 sensilles sur les mamelons des palpes gnathochilariaux, 12 et 13 sensilles sur les expansions latérales (Fig. 29) : la pseudo-articulation des sensilles est difficile à observer à ce stade juvénile.

Telson.- Plages subcirculaires comprenant 4 grosses embases de trichomes *c*, et 6 trichomes *a* formant les groupes latéraux.

AFFINITÉS. — Voisin de *M. enghoffi* n. sp., par le nombre et la disposition des sensilles basiconiques du 6ème article antennaire, il s'en distingue par la forme de ces phanères qui sont plus longs et plus grêles, et par les soies des subcoxas (Fig. 30), des coxas et des trochanters dont le funicule est pubescent et proportionnellement plus court. Les dents accessoires de la griffe paraissent plus trapues que celles de *M. enghoffi,* mais un adulte de cette forme incertaine serait nécessaire pour la comparer à *M. enghoffi* .

Anopsxenus caboverdus n. sp. (Figs. 10-14)

(= *Anopsxenus indicus* in : ENGHOFF, 1993)

REMARQUE. — Lors d'une première identification, j'avais rapporté les spécimens du Cap Vert à une espèce décrite de Bombay, *Anopsxenus indicus* Condé et Jacquemin, 1963, type et seul représentant du genre. Toutefois, un examen plus attentif m'a conduit à considérer qu'il s'agit en fait d'une espèce distincte qui est décrite ici.

Source : MNHN, Paris

STATION. — Santiago. S. Jorge dos Orgaos, n° 2228, VII.1989, A. VAN HARTEN leg. : 2 femelles à 13 pp (ad.), 2 ind. à 6 pp., 1 ind. à 5 pp., 1 ind. à 3 pp.

DESCRIPTION. — Les adultes sont désignés respectivement comme holotype et paratype. La tête disséquée de l'holotype, montée dans l'Euparal, préparation n° 1363, est conservée au Musée de Zoologie de Copenhague ; son corps est monté dans le Médium II de Marc André, ainsi que le paratype et les juvéniles.

Adultes.

Longueurs.- Corps du paratype (sans le pinceau caudal) = 2,30 mm. Pinceau caudal = 0,25 mm. 2ème tarse de la 13ème paire de pattes = 150 (holotype) et 143 µm.

Téguments.- Aucune trace de pigment n'est décelable.

Tête.- Plages postérieures du vertex allongées, plus de trois fois plus longues que leur écartement, comprenant chacune une rangée antérieure de 18 trichomes et une postérieure de 4 (paratype). Les antennes sont conformes à la définition du genre (3 et 2 sensilles basiconiques respectivement en VI et VII, mais le cœloconique manque en VI et il est dédoublé en VII (Fig. 10), ce qui est typique des antennes régénérées (une antenne à 7 articles du paratype est en cours de régénération) (NGUYEN DUY - JACQUEMIN, 1972).

Trichobothries, labre et gnathochilarium (Fig. 12) comme chez *A. indicus*. 19 et 20 sensilles sur les mamelons du gnathochilarium (paratype).

Tronc.- Plages latérales du collum avec 66 et 70 trichomes (holotype) ; aux tergites suivants, les plages comprennent de 35 à 48 trichomes et sont unies par une rangée marginale ininterrompue de 40 à 48 trichomes (holotype).

Pilosité des pattes identique à celle de *A. indicus*, mais les vulves portent de 13 à 16 soies, arquées pour la plupart, et différentes en cela de celles portées par les subcoxas, coxas et trochanters (Fig. 11). Rapport tarse/griffe = 10 aux pattes XII et XIII, 9 à la patte I de la femelle paratype. Les denticules situés à la base de la griffe sont bien développés, le postérieur de longueur égale au 1/3 de la griffe qui possède une faible dent sternale (Fig. 14).

Telson.- Groupes latéraux avec 9 et 10 trichomes *a*.

Immatures : Stades I, III et IV.

Le 6ème article antennaire du stade I (3 pp.) n'a que 2 sensilles basiconiques et un sensille cœloconique postérieur ; le 3ème sensille basiconique, antérieur aux 2 autres, n'apparaît qu'aux stade II ou III ; il est présent en effet chez l'individu à 5 pp.

7 sensilles sur les expansions des palpes gnathochilariaux et 20 à 22 sensilles sur les mamelons. Nombre de trichomes des plages postérieures de la tête augmentant avec la croissance : 6+2 au stade I, 8-9+2 au stade III, 9-10+2 au stade IV ; il en est de même pour les trichomes *a* du tergite telsonien : 5+5 (stade I), 7+7 (stade II), 8+9 (stade III). Les trichomes *C2* et *b* du telson sont présents chez les larves III et IV ; ce mode d'acquisition est probablement identique à celui observé chez *Monographis tamoyoensis* et *Pauropsxenus vilhenae* où ces trichomes n'apparaissent qu'au stade III (NGUYEN DUY - JACQUEMIN, 1973).

AFFINITÉS. — *Anopsxenus* Condé et Jacquemin, 1963, a pour type le seul polyxénidé aveugle et pigmenté connu. Un pigment brun qui occupe des plages de forme définie sur la tête, le tronc et les pattes, a subsisté après un séjour de 3 années en alcool. *Anopsxenus indicus,* récolté à Bombay par P. REMY en 1959, est représenté par une femelle à 12 pp., choisie comme lectotype en raison d'un meilleur état de conservation, et une femelle paralectotype à 13 pp. (ad.).

La nouvelle espèce est totalement dépourvue de pigmentation et il n'y a aucune preuve que le séjour en alcool ou l'exposition à la lumière aient été responsables de la destruction d'un pigment. Les griffes courtes (rapport tarse/griffe = 10 vs 6,4 chez *A. indicus*) et trapues, à volumineux denticules basilaires et à petite dent sternale, sont très différentes des griffes longues et grêles de *A. indicus*, présentant de minuscules denticules à leur base (Figs. 14, 15). Les nombreux phanères des vulves manquent chez *indicus*. Enfin, le 6ème article antennaire est plus allongé chez *caboverdus* que chez *indicus* : rapport L/l = 1,40-1,60 et 1,70-1,80 vs 1,13-1,28

Source : MNHN, Paris

pour le lectotype de *indicus*, on notera cependant qu'il s'agit d'antennes régénérées pour *caboverdus*.

Ces différences nous paraissent justifier le statut spécifique accordé à présent aux spécimens du Cap Vert.

TABLEAU 1. — Liste des espèces de Macaronésie.
TABLE 1. — Check-list of Macaronesian species.

Familles	Espèces	CANARIES	CAP VERT	MADERE	AÇORES
	Polyxenus fasciculatus	Gran Canaria Tenerife Gomera Hierro		Madeira Selvagem Grande	
	Polyxenus lagurus (forme bisexuée)				São Miguel Pico
POLYXENIDAE	*Polyxenus oromii* n. sp.	Fuertoventura La Palma Tenerife			
	Macroxenus enghoffi n. sp.	Fuertoventura			
	Macroxenus cf. *enghoffi*		S. Antão		
	Anopsxenus caboverdus n. sp.		S. Tiago		
LOPHOPROCTIDAE	*Lophoproctinus inferus maurus*	Fuertoventura Gran Canaria Tenerife			
	Lophoturus madecassus		S.Tiago		

FAMILLE DES LOPHOPROCTIDAE

Lophoproctinus inferus maurus Marquet & Condé, 1950.

STATIONS. — Fuertoventura. Jandia : Barranco del Ciervo, Morro de Cavedero N of Morro Jable, grassy, stony W slope, 700 m, *Astericus* etc., under stones n°2660 : 6 femelles à 13 pp. (ad.), 1 femelle à 12 pp., 1 femelle à 10 pp., 1 individu à 8 pp. — Localité précédente, grassy ridge and N & E slopes, 700 m, *Astericus*, etc., under stones, n° 2631, 4.I.1990 : 2 femelles à 13 pp. (ad.). — Gran Canaria . Roque Bentayga, SW slope, 1100 m, *Euphorbia obtus*, Kleinia, under deeply imbedded stone, n° 2632, 1.I.1990 : 1 mâle à 13 pp. (ad.). Tous récoltés par M. BÂEZ, H. ENGHOFF. — Tenerife. Barranco de Las Cuevas, Teno Alto, 5.XI.1989 : 1 femelle à 13 pp. (ad.), R. RODRIGUEZ leg.

RÉPARTITION. — Cette sous-espèce, décrite d'Algérie (Dar-el-Oued) par MARQUET & CONDÉ (1950), se distingue de la forme typique, connue d'Italie aux environs de Portici (SILVESTRI, 1903), par sa chétotaxie céphalique et la présence d'une dent dans la concavité de la griffe. Elle a été retrouvée en Algérie (Blida), au Maroc occidental (Safi, Sidi Kacem, Marrakech) et oriental (Oudja), et en Tunisie (Le Kef) (CONDÉ, 1954).

Source : MNHN, Paris

Lophoturus madecassus Marquet & Condé, 1950.

Cette espèce, signalée de Santiago (île du Cap Vert) par ENGHOFF (1993), présente une très vaste répartition circum-tropicale : décrite de Madagascar (Tuléar), elle a été signalée d'Afrique (Hoggar, Côte d' Ivoire), des Antilles (Jamaïque), de Floride (Dry Tortugas) et d'îles du Pacifique Sud (Archipel des Tonga, Atoll Suvorov).

BIOGÉOGRAPHIE

Deux espèces à large répartition géographique sont présentes aux Canaries : *Polyxenus fasciculatus* et *Lophoproctinus inferus maurus* (Fig. 31).

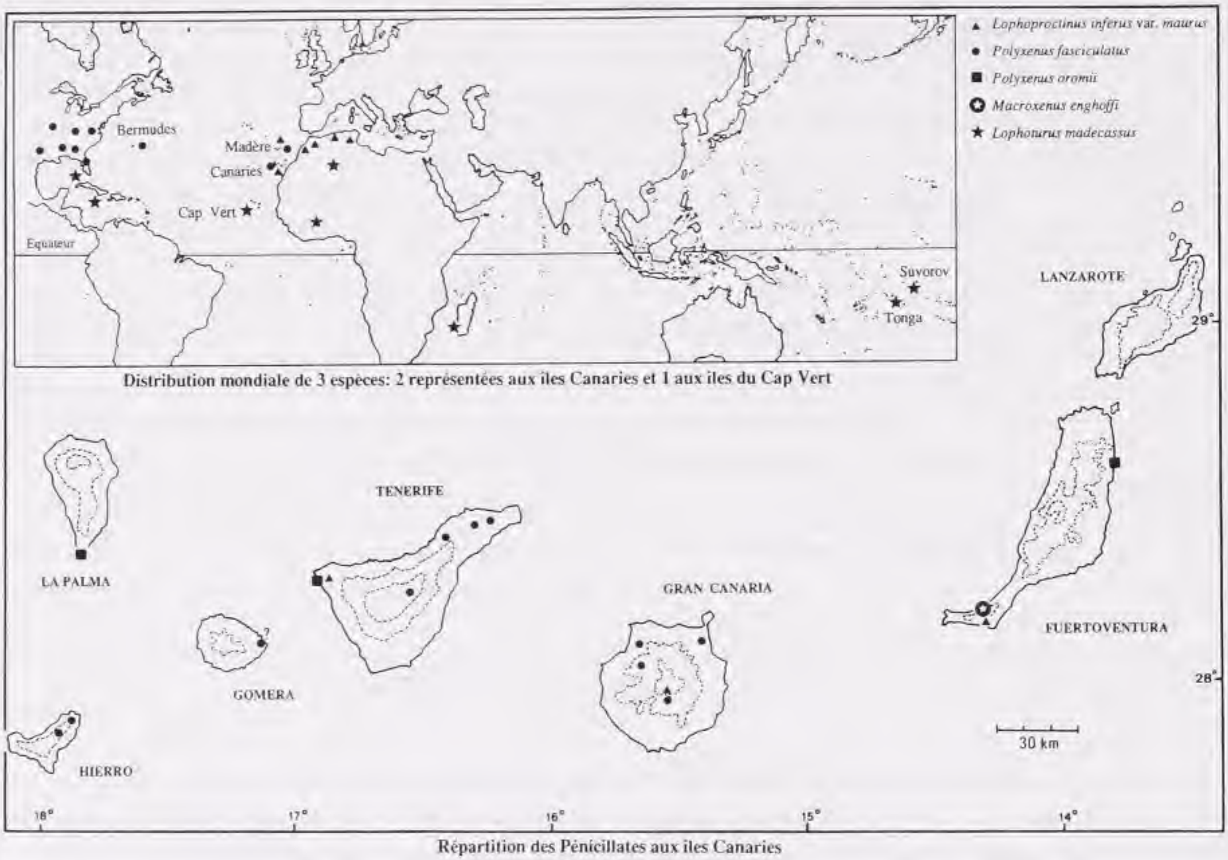


FIG. 31. — Répartition locale et mondiale des espèces de pénicillates des îles Canaries et du Cap Vert.
FIG. 31. — Local and world distribution of Penicillata species of Canary Islands and Cape Verde Islands.

Source : MNHN, Paris

P. fasciculatus est l'espèce la plus répandue aux Canaries, peuplant 13 stations : 2 à Hierro, 1 à Gomera, 6 à Tenerife et 4 à Gran Canaria. Elle occupe la portion méridionale de l'Amérique du Nord (Centre et Sud-Est des Etats-Unis), les Bermudes et Madère (Ribero Seco, Pico do Gato, Selvagem Grande), alors que la forme bisexuée de *P. lagurus* est implantée en Eurasie et aux Açores (CONDÉ & NGUYEN DUY - JACQUEMIN, 1994) où elle a été identifiée à São Miguel par CONDÉ (1961) et plus récemment, par moi-même, à Pico, sur des rochers de laves à Costa Cachorro (leg. OROMI 1987). On notera que si l'Archipel des Açores est plus éloigné de l'Europe que les îles Canaries et que Madère, il est en revanche plus septentrional. La limite géographique entre ces deux espèces n'est pas précisée, mais on ne les a jamais vu cohabiter. La forme parthénogénétique de *P. lagurus* est présente dans le Nord de l'Amérique et de l'Eurasie ; elle paraît mieux adaptée aux climats continentaux (CONDÉ & NGUYEN DUY - JACQUEMIN, 1994) et la température moyenne pourrait être aussi le facteur limitant l'extension, vers le Nord, de *P. fasciculatus* (ce qui est net aux États-Unis), comme celle de *P. lagurus* bisexué en Eurasie.

Lophoproctinus inferus maurus a été récolté sur 3 des îles Canaries : Fuertoventura, Gran Canaria et Tenerife ; elle est connue sur le continent le plus proche, l'Afrique du Nord (Maroc, Algérie, Tunisie), située à 90 km de Fuertoventura.

Autre exemple d'espèce à large répartition géographique, *Lophoproctus madecassus*, le seul pénicillate à 11 paires de pattes, signalé par ENGHOFF (1993) de Santiago (Cap Vert) est une espèce tropicale : Hoggar, Côte d'Ivoire, Madagascar, Floride, Jamaïque, Pacifique Sud (Tonga, Suvorov).

Les espèces nouvelles trouvées aux Canaries peuvent-elles être considérées comme des endémiques? *M. enghoffi* est éloigné de *M. rubromarginatus*, d'Afrique septentrionale et de *M. caingangensis*, du Brésil, par la disposition des sensilles du VIe article antennaire. *Anopsxenus. caboverdus*, en revanche, est voisin de la seule autre espèce du genre, *A. indicus*, de Bombay. *Polyxenus oromii* enfin est très proche de *P. chalcidicus*, du Bassin de la Méditerranée (Grèce, Israël). Deux spécimens à 10 pp. (mâle et femelle) de Karpathos (Pigadia, 12.IV.52, H. SCHMALFUSS leg.), déterminés par B. CONDÉ, sont rapportés sous réserve, à cette espèce, dans l'attente de spécimens adultes.

REMERCIEMENTS

J'adresse mes plus vifs remerciements à Monsieur le Professeur B. CONDÉ pour ses conseils dans la rédaction de ce manuscrit et à Jacques REBIÈRE pour la réalisation de l'iconographie.

RÉFÉRENCES

BRÖLEMANN, H. W., 1896. — Myriapodes provenant des Campagnes scientifiques de l'*Hirondelle* et de la *Princesse Alice*. *Bull. Soc. zool. Fr.*, **21** : 198-204.

CONDÉ, B. , 1950. — Un diplopode nouveau pour la France. *L'Entomologiste*, **6** : 109-116.

CONDÉ, B. , 1953. — Diplopodes Pénicillates de Corse. *Bull. Soc. zool. Fr.*, **78** : 33-35.

CONDÉ B., 1954. — Diplopodes Pénicillates d'Afrique septentrionale. *Bull. Mus. natl. Hist. nat., 2ème Ser.*, **26** : 496-500.

CONDÉ, B., 1961. — Diplopodes Pénicillates des Açores et de Madère. *Bol. Mus. municipl. Funchal*, **14** : 7-10.

CONDÉ, B., 1970. — Essai sur l'évolution des Diplopodes Pénicillates. *Bull. Mus. natl. Hist. nat., 2ème Ser.*, **41**, suppl. 2 : 48-52.

CONDÉ, B., 1971. — Diplopodes pénicillates des nids brésiliens de *Camponotus rufipes*. *Rev. Ecol. Biol. Sol*, **8** : 631-634.

CONDÉ, B., 1972. — Présence aux Bermudes de Diplopodes Pénicillates et d'Arachnides Palpigrades. *Rev. Ecol. Biol. Sol*, **9** : 127-129.

CONDÉ, B. & MASSOUD, Z., 1974. — Diplopodes Pénicillates du Brésil et de la République Argentine. *Rev. Ecol. Biol. Sol.*, **11** : 223-232.

CONDÉ, B. & NGUYEN DUY - JACQUEMIN, M., 1971. — Pénicillates d'Israël rassemblés par G. Levy. *Bull. Mus. natl. Hist. nat., s. D*, **42** : 1251-1258, 1970.

CONDÉ B. & NGUYEN DUY - JACQUEMIN, M., 1990. — Découverte d'un caractère sexuel secondaire nouveau chez le mâle d'un Polyxénidé (Myriapodes, Pénicillates). *Ber. nat.-med. Verein Innsbruck*, **suppl. 10** : 57-62.

Source : MNHN, Paris

CONDÉ B. & NGUYEN DUY - JACQUEMIN, M., 1994. — Parthénogenèse et reproduction bisexuée dans le complexe de *Polyxenus lagurus* (L.). *Biogeographica*, **70** : 41-48.

ENGHOFF, H., 1993. — Cape Verdean millipedes (Diplopoda). *Tropical. Zool.*, **6** : 207-216.

ENGHOFF, H. & SCHEMBRI, J., 1989. — The Millipedes of the maltese islands (central mediterranean). *Boll. Soc. ent. ital., Genova,* **120** : 164-173.

MARQUET M. L. & CONDÉ, B., 1950. — Contribution à la connaissance des Diplopodes Pénicillates d'Afrique et de la Région madécasse. *Mém. Inst. sci. Madagascar* , sér. A, **4** : 113-134.

NGUYEN DUY - JACQUEMIN, M., 1972. — Régénération antennaire chez les larves et les adultes de *Polyxenus lagurus* (Diplopode, Pénicillate). *C. R. Acad. Sc. Paris (D)*, **274** : 1323-1326.

NGUYEN DUY - JACQUEMIN, M., 1973. — Contribution à la connaissance de l'anatomie céphalique, des formations endocrines et du développement postembryonnaire de *Polyxenus lagurus* (Diplopodes pénicillates). Thèse Doctorat d'état ès-Sciences naturelles, UPMC, Paris VI, 148 pp.

NGUYEN DUY - JACQUEMIN, M., 1976. — Étude de la variabilité des caractères de deux espèces du genre *Polyxenus*, *P. lagurus* (L.) et *P. fasciculatus* Say (Diplopode Pénicillate), basée sur les mensurations d'articles tarsaux. *Bull. Mus. natl. Hist. nat. Paris, 3ème Ser., Zool. 249*, **356** : 105-118.

NGUYEN DUY - JACQUEMIN, M. & CONDÉ, B., 1984. — Nouvelle description et statut de *Polyxenus bartschi* Chamberlin (Diplopodes, Pénicillates). *Bull. Mus. natl. Hist. nat., Paris,4ème Ser.*, **6**, A, 3: 721-728.

SILVESTRI, F., 1903. — *In* : BERLESE, *Acari, Myriapoda et Scorpiones hucusque in Italia reperta*. Fasc. **98**, n° 4.

VERHOEFF, K. W., 1921. — Ueber Diplopoden der Riviera und einige alpenädische Chilathognathen. *Arch. natg. Berlin*, **87 A** : 1-110.

VERHOEFF, K. W., 1941. — Zur Kenntnis der *Polyxenus*-Arten. *Zool. Anz.*, **133** : 259-264.

VERHOEFF, K. W., 1952. — Weitere Beiträge zur Kenntnis der Isopoden- und Diplopodenfauna von Ischia und Capri. *Bonn. Zool. Beitr.*, **3** : 125-150.

Source : MNHN, Paris

Une approche des Diplopoda Penicillata de l'Amérique du Nord

***Bruno* CONDÉ**

Musée de Zoologie, 34 rue Sainte-Catherine, F-54000 Nancy, France

RÉSUMÉ

Neuf espèces ou sous-espèces nominales de Diplopoda Penicillata ont été répertoriées en Amérique, au nord du Mexique, et attribuées, à une exception près, au genre holarctique *Polyxenus*. Trois d'entre elles sont actuellement inclassables, mais les six autres ont fait l'objet d'une révision. Quatre espèces appartiennent de fait au genre *Polyxenus* (*anacapensis, fasciculatus, lagurus, pugetensis*), une au genre subtropical *Macroxenodes* (*bartschi*) et une au genre *Lophoturus* (*madecassus*). Nous ajoutons ici une seconde espèce (cf. *aequatus*) à ce dernier genre. Un néotype de *P. fasciculatus*, la première espèce américaine décrite, est désigné afin d'éviter toute confusion avec les formes bisexuée ou parthénogénétique de *P. lagurus*.

ABSTRACT

An approach to the Diplopoda Penicillata from North America.

Nine nominal species or subspecies of Diplopoda Penicillata have been recorded from America, north of Mexico, and assigned , with one exception, to the holarctic genus *Polyxenus*. Three of them are unclassifiable for the time, but the six others were revised. Four of them belong in fact to *Polyxenus* (*anacapensis, fasciculatus, lagurus, pugetensis*), one to the subtropical genus *Macroxenodes* (*bartschi*) and one to the wide ranging genus *Lophoturus* (*madecassus*). We add here a second species (cf. *aequatus*) of the last genus. A neotype of *P. fasciculatus*, the first described american species, is designed to avoid confusions with the bisexual or parthenogenetic stocks of *P. lagurus*.

INTRODUCTION

Neuf formes nominales de Penicillata ont été décrites ou citées d'Amérique septentrionale au nord de Mexico. Ce sont, dans l'ordre chronologique :

1- *Polyxenus fasciculatus* Say, 1821. Southern States
2- *Polyxenes* (sic) *fasciculatus* var. *pallidus* Ryder, 1878. Maryland
3- *Polyxenus pugetensis* Kincaid, 1898. Westerns Washington
4- *Polyxenus bartschi* Chamberlin, 1922. Florida (Tortugas)
5- *Polyxenus lagurus* (L.). Nova Scotia
6- *Polyxenus fasciculatus* var. *victoriensis* Pierce, 1940. Texas (Victoria)
7- *Polyxenus anacapensis* Pierce, 1940. California (Anacapa Is.)
8- *Polyxenus tuberculatus* Pierce, 1940. Texas (Sabinal)
9- *Lophoturus madecassus* (Marquet et Condé, 1950). Florida (Loggerhead Key)

CONDÉ, B., 1996. — Une approche des Diplopoda Penicillata de l'Amérique du Nord. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 127-135. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

Nous y ajoutons :

10- *Lophoturus* cf. *aequatus* (Loomis, 1936). Florida (Key Largo).

Polyxenus bartschi a été attribué à *Macroxenodes* (NGUYEN DUY - JACQUEMIN & CONDÉ, 1984) et les caractères des trichomes telsoniens écartent aussi *fasciculatus victoriensis* et *tuberculatus* du genre *Polyxenus*, sans que l'on puisse leur assigner une position générique convenable en l'absence d'un nouvel examen du matériel typique. En revanche, il est probable que *fasciculatus pallidus* soit un *Polyxenus* authentique.

ÉNUMÉRATION

Polyxenus fasciculatus Say, 1821 (Fig. 1A, B, C)

La description originale, citée par PIERCE (1940), ne permet pas de reconnaître l'espèce, aucun type n'est connu et la mention "Inhabits the Southern States" rendait fort incertaine la recherche de topotypes. Il existe heureusement une biographie de SAY, consultée pour nous par le Dr. Richard L. HOFFMAN, qui précise que SAY n'a effectué qu'une seule expédition dans les Etats du Sud avant 1821, de Philadelphie à Savannah (Georgia) et jusqu'au Nord-Est de la Floride, en suivant les îles côtières, où il a récolté de nouvelles espèces d'Insectes. HOFFMAN (*in litt.*10.02.65) conclut : "the locus typicus of *P. fasciculatus* Say is the costal part of Georgia, between Savannah and Jacksonville".

NÉOTYPE.

Devant la nécessité de désigner un néotype, en raison d'une situation confuse entre cette espèce et les lignées bisexuée ou parthénogénétique de *Polyxenus lagurus*, le Dr. HOFFMAN nous a communiqué un mâle adulte (13 pp.) étiqueté : "Georgia : Glynn County : St. Simon's Island, Brunswick, 19 june 1977 R. L. HOFFMAN leg.", déposé au Laboratoire de Zoologie, Arthropodes, du Muséum national d'Histoire naturelle de Paris.

Longueurs.- Corps = 2,06 mm (extension moyenne) ; pinceaux telsoniens = 0,54 mm (trichomes en crosses) et 0,68 mm (trichomes barbelés) ; ta I = 89,7 µm, ta XIII = 105 µm, ta XIII/ta I = 1,17.

Tête.- Plages postérieures du vertex 3 fois plus longues que leur écartement (92-95/30) comprenant une rangée antérieure de 13 et 15 trichomes dirigés vers l'avant et une rangée postérieure de 8 dirigés vers l'arrière ; une paire de trichomes parasagittaux en arrière des plages. Calice de la trichobothrie la plus interne beaucoup plus petit que les autres. 6 stemmates subégaux.

6ème article antennaire environ 1 fois 1/10 plus long que large (L/1 = 1,11) (Fig. 1A). A l'antenne gauche, 8 sensilles basiconiques, dont un épais, entre un sensille sétiforme à base renflée antérieur et un sensille coeloconique postérieur ; le basiconique épais, plus court que ses voisins, est situé dans la moitié antérieure du groupe et entouré de 7 basiconiques grêles[1]. L'antenne droite, atypique, est dépourvue du basiconique épais. Article VII avec 4 basiconiques (2 grêles, 2 épais) et un coeloconique (Fig. 1B, C).

Marge antérieure du labre pourvue de lamelles hyalines imbriquées, non dénombrables avec certitude chez ce spécimen fortement éclairci. Face externe couverte de granules à courte pointe apicale, ceux des premières rangées marginales plus gros que les suivants.

Palpes du gnathochilarium avec 14 sensilles à gauche et 12 à droite sur l'expansion latérale[2], et 17 sur le mamelon.

---

1 Le nombre total de sensilles basiconiques grêles varie de 7 à 17 selon les individus et les populations (NGUYEN DUY - JACQUEMIN, 1976 : 113, TABLEAU 4).

2 De 10 à 15 dans les proportions suivantes : 1, 14, 139, 9, 4, 1 (NGUYEN DUY - JACQUEMIN, 1976 : 115).

Source : MNHN, Paris

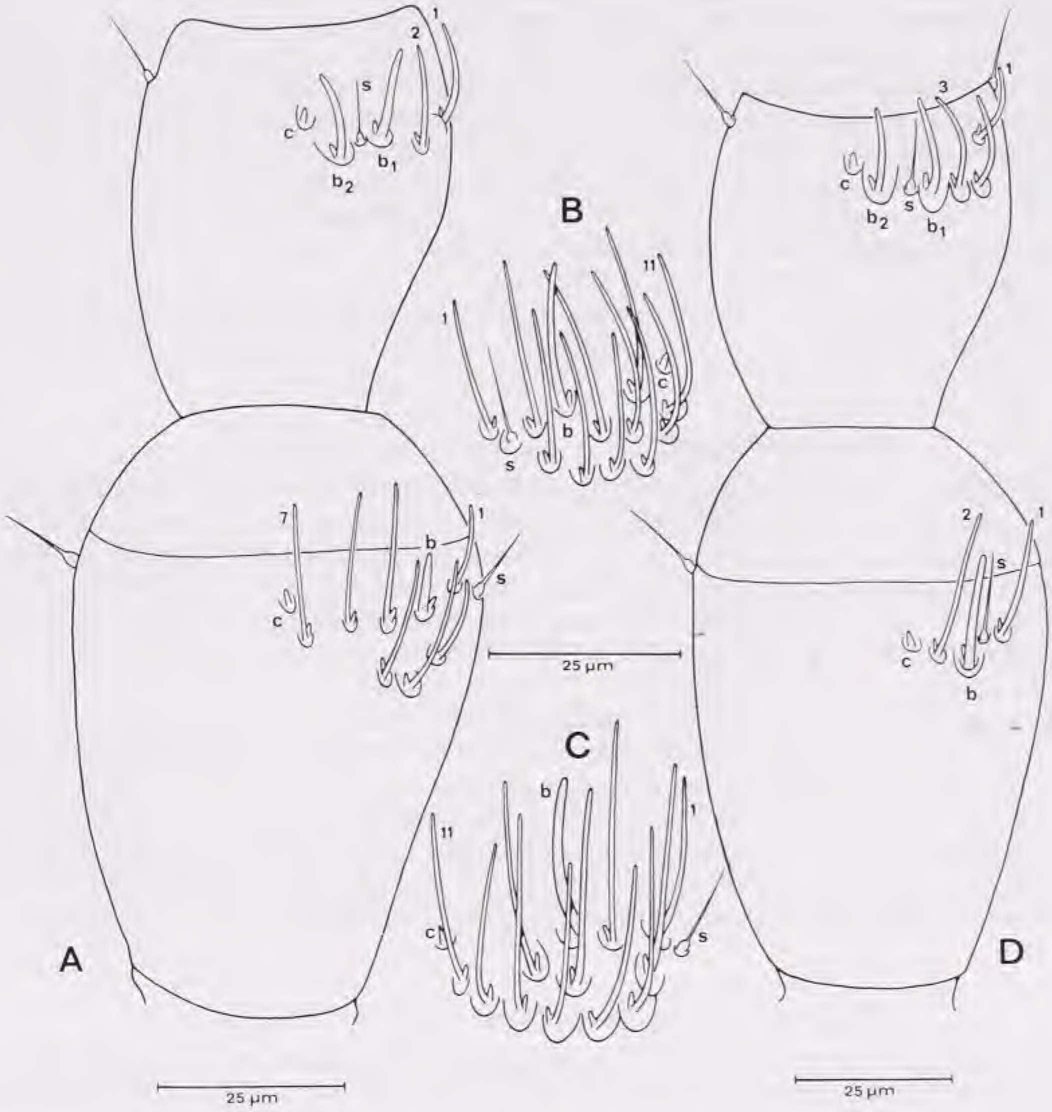


FIG. 1. — *Polyxenus fasciculatus* Say. A : articles VI et VII de l'antenne gauche du néotype, face tergale. B : sensilles de l'article VI droit d'un mâle adulte de St Bernard Pa, Louisiane. C : sensilles de l'article VI gauche d'une femelle adulte de Bâton Rouge, Louisiane.- *Polyxenus pugetensis* Kincaid, femelle adulte de Oak Creek, Oregon. D : articles VI et VII de l'antenne gauche, face tergale. 1-11 = sensilles basiconiques grêles ; b-b_2 = sensilles basiconiques épais ; c = sensille coeloconique ; s = sensille sétiforme à base renflée.

FIG. 1. — Polyxenus fasciculatus *Say. A: left antennal articles VI and VII of the neotype, tergal side. B: sensilla of the right article VI in an adult male from St Bernard Pa, Louisiana. C: sensilla of the left article VI of an adult female from Baton Rouge, Louisiana.* Polyxenus pugetensis *Kincaid, adult female from Oak Creek, Oregon. D: left antennal article VI and VII, tergal side. 1-11 = thin basiconic sensilla ; b-b_2 = thick basiconic sensilla; c = coeloconic sensilla; s = setiform sensilla with a bulbous base.*

Tronc.- Chétotaxie tergale du type de *P. lagurus*, les trichomes des deux rangées marginales étant toutefois disposés moins régulièrement.

Épine du 2ème article du tarse et griffes comme chez *P. lagurus*. Invaginations glandulaires sur les subcoxas VIII et IX.

Source : MNHN, Paris

Telson.- Trichomes des plages subtriangulaires médio-dorsales : 22 et 21. Trichomes principaux des pinceaux terminés en une crosse appendiculée.

Répartition.- J'ai déterminé l'espèce des États suivants : Illinois, District of Columbia, North Carolina, Tennessee, Florida, Alabama, Arkansas, Mississippi, Louisiana et Texas, outre le néotype de Georgia. Au total : 175 spécimens répartis entre 21 mâles et 44 femelles à 13 pp. (ad.), 8 mâles et 24 femelles à 12 pp., 10 mâles et 8 femelles à 10 pp., 8 ind. à 10 pp. de sexe non reconnu, 8 ind. à 8 pp., 9 ind. à 6 pp., 12 ind. à 5 pp., 10 ind. à 4 pp., 13 ind. à 3 pp.

La sex-ratio est de 0,51 sur 115 individus (39 mâles et 76 femelles). Toutes les populations dont l'échantillonage est suffisant renferment des représentants des deux sexes, à l'exception de Boca Raton, Florida (13 femelles).

L'espèce peuple aussi les Bermudes (St George's West, CONDÉ, 1972), Madère (CONDÉ, 1961, sous le nom de *P. lagurus*) et les Canaries (CONDÉ & NGUYEN DUY - JACQUEMIN, 1993).

Polyxenus lagurus (L.), lignée parthénogénétique

J'ai déterminé l'espèce des États suivants : Massachusetts, New Jersey, Michigan, Illinois, Montana, Washington, Colorado, Arizona. Au total : 116 spécimens : 55 femelles (32 à 13 pp. (ad.), 15 à 12 pp., 8 à 10 pp.), 26 ind. à 8 pp., 17 ind. à 6 pp., 10 ind. à 5 pp., 6 ind.à 4 pp., 2 ind. à 3 pp. Tous sont identiques aux spécimens européens de la lignée parthénogénétique, la disposition et le nombre des sensilles basiconiques du 6ème article antennaire (4 à 6 grêles, 5 le plus souvent, NGUYEN DUY - JACQUEMIN, 1976 : 114) permettant de les distinguer facilement de *P. fasciculatus*.

On ne connaît pas encore d'aires de contact entre *P. lagurus* et *P. fasciculatus*, comme cela existe au Nord de l'Europe occidentale entre les lignées parthénogénétique et bisexuée de *P. lagurus*. Les stations les plus proches des deux espèces sont situées dans l'Illinois, à quelque 600 km de distance. La limite méridionale de *P. lagurus* coïncide, de façon assez satisfaisante, avec celle du climat continental défini par des amplitudes de température supérieures à 20°C. Il n'est pas possible de décider actuellement si la présence de *P. lagurus* en Amérique du Nord est la conséquence d'une répartition holarctique ancienne ou si elle est due à une intervention de l'Homme.

Polyxenus pugetensis Kincaid, 1898 (Fig. 2)

Selon son auteur, cette espèce serait beaucoup plus proche de *P. lagurus* que de *P. fasciculatus*. Le nom fait référence à la localité de Puget (ou au Puget Sund), à l'ouest de Seattle, tandis qu'une indication plus vague figure dans la description originale : "Hab. : Westerns Washington". L'auteur précise qu'il n'a observé que des femelles, ce qui suggère une possible confusion avec la lignée parthénogénétique de *P. lagurus* qui est présente au moins dans l'Est de l' Etat (Spokane).

COTYPE.

Le Dr. F. RICHARDSON nous a communiqué une lame qui porte les indications suivantes :

"*Polyxenus pugetensis* Kincaid, cotype", "Thomas Burke Memorial-Washington State Museum, Seattle, Washington. Catalogue n° 20344","Sex...-Date 1897-Local. University of Washington Campus, Seattle, Washington".

Il s'agit d'une femelle à 13 pp. (ad.), montée dans le Baume du Canada. L'épaisseur de la préparation et l'opacité du spécimen rendent l'observation très difficile, mais j'ai pu distinguer néanmoins l'apex de 3 sensilles basiconiques seulement sur le 6ème article antennaire.

SPÉCIMENS COMPLÉMENTAIRES. — Communiqués par la regrettée Dr. Nell B. CAUSEY et le Dr. R. L. HOFFMAN.

Washington. Mason Co., 1 mi E Lake Cushman Dam, Olympic Pen., 07.07.1959, L. M. Smith : 1 mâle à 13 pp. (ad.). — Oregon. Benton Co. Moss sample (Berlese), 03.1962, L.

Source : MNHN, Paris

Abrahamsen : 1 femelle à 13 pp. (ad.).- Oak Creek, 6 mi NW Corvallis, Oak/Douglas fir litter, 29.04.1972, L. Russell : 11 mâles et 11 femelles à 13 pp. (ad.), 1 mâle et 1 femelle à 12 pp., 3 ind. à 8 pp., 4 ind. à 6 pp.

Adultes. Longueurs.- Corps = 3,00-3,60 mm ; pinceaux telsoniens = 0,48 mm (trichomes en crosses) et 0,65 mm (trichomes barbelés). Ta I : mâles = 100-111 µm ($\bar{x}$ = 104,8 µm, n = 10) ; femelles = 100-117,5 µm ($\bar{x}$= 110,3 µm, n = 9). Ta XIII : mâles = 110,3-127,8 µm ($\bar{x}$ = 119,9 µm, n = 10) ; femelles = 125,8-140,2 µm ($\bar{x}$ = 132,6 µm, n = 10). Ta XIII/ta I: mâles = 1,09-1,27 ($\bar{x}$ = 1,15 ; n = 9) ; femelles = 1,17-1,28 ($\bar{x}$ = 1,20 ; n =9).

Tête.- Plages postérieures du vertex environ deux fois à deux fois et demi plus longues que leur écartement, comprenant chacune 19 à 27 (21-24 le plus souvent) phanères sur 2 rangs rapprochés ; 1+1 trichomes parasagittaux en arrière.

Les articles antennaires ressemblent à ceux de *P. lagurus* ou de *P. fasciculatus* par leurs longueurs relatives et leur forme. En revanche, les sensilles basiconiques du 6ème article sont au nombre de 3 seulement, le médian un peu plus épais et plus court que les autres ; en outre, un sensille sétiforme à base renflée et un coeloconique sont présents, comme chez les deux espèces précédentes.

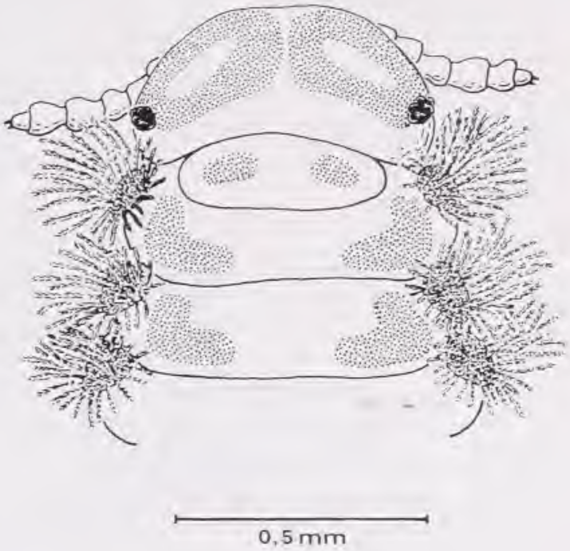


FIG. 2. — *Polyxenus pugetensis* Kincaid, femelle adulte : plages pigmentaires de la tête et des trois premiers tergites. Dessin de Claude POIVRE.

FIG. 2. — Polyxenus pugetensis *Kincaid, adult female: pigmentary areas on the head ant the first three tergites. Drawing by Claude POIVRE.*

Article VII avec 3 sensilles basiconiques grêles, suivis de 2 plus épais et d'un coeloconique (Fig. 1D).

6 stemmates subégaux. Trichobothrie antéro-interne, à calice de dimensions réduites, qui a échappé à KINCAID.

Labre avec 6+6 lamelles marginales imbriquées, les tubercules des 2-3 premiers rangs beaucoup plus volumineux que les suivants.

Palpes du gnathochilarium portant 15 sensilles le plus souvent (n = 23), rarement 16 ou 17 (n = 2) et 13 ou 14 (? phanères non vus, arrachés ou réellement absents) ; 15 sensilles aux palpes des deux individus à 12 pp., 12 et 9 chez les individus à 8 et 6 pp.

Tronc.- Les plages latérales du collum sont unies par deux rangées postérieures ininterrompues de trichomes dirigés vers l'arrière ; une courte rangée antérieure et une rangée intermédiaire sont interrompues en leur milieu.

Aux tergites suivants, les phanères des deux rangées marginales, mais surtout ceux de la rangée postérieure (dirigés vers l'arrière) sont insérés suivant une ligne brisée, ce qui provoque un dédoublement plus ou moins régulier des rangées et l'impression d'une troisième rangée intermédiaire.

Telson.- Trichomes des plages subtriangulaires médio-dorsales : mâles 14+14 - 16+16 (15 le plus souvent) ; femelles 16+16 - 21+22 (16 le plus souvent).

Source : MNHN, Paris

Polyxenus anacapensis Pierce, 1940 (Fig. 3)

Décrite de Middle Anacapa Island (California), j'ai pu examiner des paratypes de cette espèce, communiqués par le Dr. Charles L. HOGUE, et établir qu'elle se distingue des autres *Polyxenus* nord-américains par la présence de 5 stemmates (vs 6) et la disposition des sensilles du 6ème article antennaire (Fig. 3B). L'espèce est bisexuée : 2 mâles et trois femelles à 13 pp. (ad.), remontés dans le médium II de Marc André, ont permis une étude détaillée.

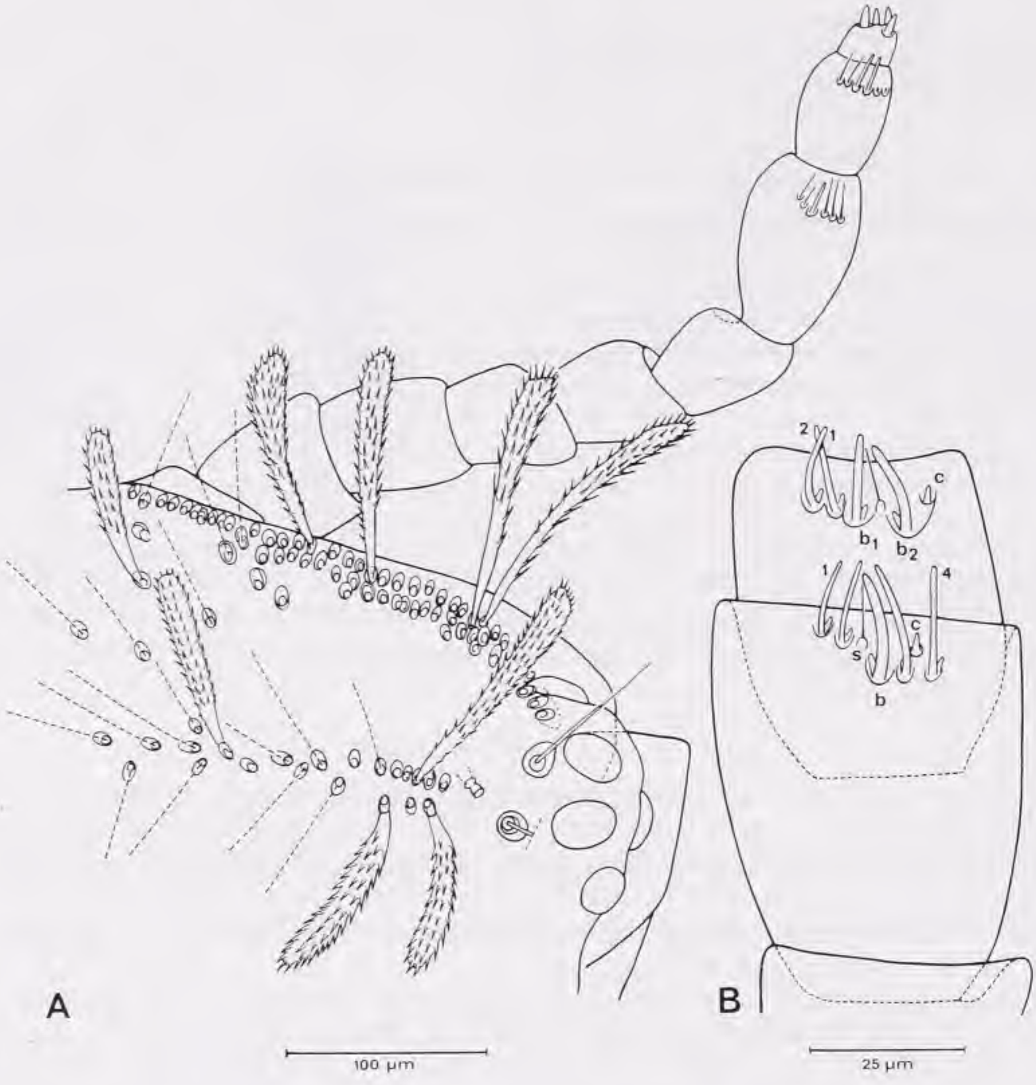


FIG. 3. — *Polyxenus anacapensis* Pierce. A : portion droite de la capsule céphalique et antenne de la femelle adulte paratype n°45 de Middle Anacapa Island. B : articles VI et VII de l'antenne droite d'un paratype adulte (sexe non identifiable) de la préparation n°20, face tergale. Chiffres et lettres comme sur la FIG. 1.

FIG. 3. — Polyxenus anacapensis *Pierce. A: right part of the head capsule and antenna of the adult female paratype n°45 from Middle Anacapa Island. B: right antennae VI & VII articles of an adult paratype (unidentifiable sex) of slide n° 20, tergal side. Symbols as in FIG. 1.*

Source : MNHN, Paris

La présence de 5 stemmates (Fig. 3A) est partagée avec 3 espèces : une du Japon (ISHII, 1983), une de Corée (ISHII & CHOI, 1988) et une autre de Chine (ISHII & LIANG, 1990) ; néanmoins, certains détails (4 à 6 sensilles basiconiques dont un épais au 6ème article de l'antenne, palpes, mandibule) rapprochent davantage *anacapensis* du complexe de *lagurus*. Une nouvelle description sera présentée ailleurs, mais dans cette attente le Tableau 1 résume les principaux caractères des quatre espèces.

TABLEAU 1. — Principaux caractères de 4 espèces de Penicillata.
TABLE 1. — Main features of 4 species of Penicillata.

	anacapensis	*shinoharai*	*koreanus*	*hangzhoensis*
Longueur du corps (mm)	2,42 - 3,01	1,80 - 2	2,35 - 2,66	1,94
Tarse 2, XIII (µm) mâle	116,5 - 120	81,20	80	100
femelle	119 - 122,5	88,75	90	—
Basiconiques ant.VI	1+ 3-5	2 + 7-9	2 + 5-9	2 + 6
ant.VII	2 + 2-3	2 + 4	2 + 3	2 + 4
Lamelles du labre	7 + 7	5 + 5	5 + 5	5 + 5
Md. éléments denticulés	ca 15	12	—	11
Palpe : mamelon	17	15	17	17
exp. latérale	11 - 12	9	9	9
Glandes subcoxales	VIII - IX	VII-VIII-IX	VIII - IX	VIII - IX
Trichomes telson mâle	24 - 26	19 - 21	30	40
Trichomes telson femelle	21 - 26	20 - 24	32	—

Macroxenodes bartschi (Chamberlin, 1922), sub ***Polyxenus***

Une nouvelle description d'après des topotypes (3 mâles et 1 femelle à 13 pp. ad.) a été proposée et un néotype (mâle à 13 pp.) a été désigné (NGUYEN DUY - JACQUEMIN & CONDÉ, 1984) et déposé au Laboratoire de Zoologie, Arthropodes, du Muséum national d'Histoire naturelle de Paris.

La localité type de l'unique spécimen décrit par CHAMBERLIN "Tortugas, Florida" est très imprécise. De deux petites séries de topotypes présumés, l'une, de Loggerhead Key, Dry Tortugas, était constituée de 6 Lophoproctidae (cf. infra) qui ne pouvaient correspondre à l'espèce recherchée ; l'autre, de Upper Snipe Keys, Lower Keys, comprenait 4 spécimens d'un Polyxenidae, le plus vraisemblablement identique à l'espèce de CHAMBERLIN, que nous avons attribués au genre *Macroxenodes*. A ce genre appartient aussi *Polyxenus pœcilus* Chamberlin 1923, dont nous avons proposé une nouvelle description d'après l'holotype de South Santa Inez Island, dans le Golfe de Californie. Le seul critère différentiel incontestable est le nombre et la disposition des sensilles basiconiques du VIe article antennaire (CONDÉ & NGUYEN DUY - JACQUEMIN, 1987).

Lophoturus madecassus (Marquet et Condé, 1950), sub ***Alloproctus***

Seule espèce de Penicillata ne possédant que 11 paires de pattes au dernier stade, elle présente une vaste répartition circumtropicale (Madagascar, Sahara, Côte d'Ivoire, Jamaïque, Floride, Pacifique central). Les spécimens de Loggerhead Key avaient été présumés être des topotypes de *Polyxenus bartschi* (NGUYEN DUY - JACQUEMIN & CONDÉ, 1984 : 722). La sex-ratio s'établit à 1/34, le seul mâle ayant été récolté sur Nomukaïki (Archipel des Tonga).

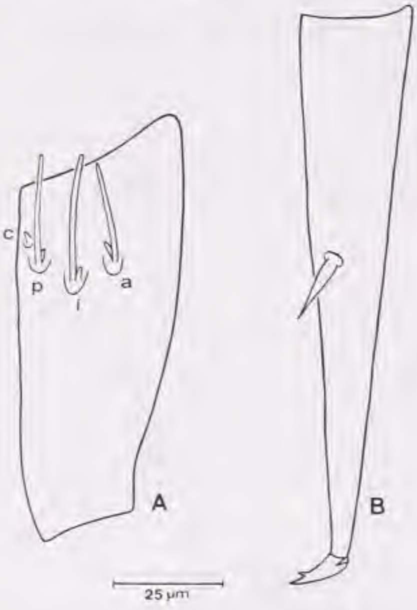
Lophoturus cf. ***aequatus*** (Loomis, 1936), sub ***Lophoproctus***

Les formes attribuées au complexe *aequatus - niveus* ont en commun un labre à marge antérieure entière, sans languettes ou formations analogues, l'ornementation de la surface externe rappelant un pavage irrégulier sans épines cuticulaires (*niveus*) ou avec une seule rangée le long du bord postérieur (*aequatus*). Les types de *aequatus* sont de Haïti, Petite Rivière de Artibonite ;

Source : MNHN, Paris

l'holotype (mâle à 13 pp.) et un paratype (mâle à 12 pp.) ont été revus et comparés à ceux de *L. niveus* (Loomis, 1936), de Beata Island (CONDÉ & TERVER, 1965).

Florida. — Key Largo, John Pennekamp St. Pk., 21.10.84, M.A.Deyrup : 1 mâle et 1 femelle à 13 pp. (ad.), 2 femelles à 12 pp.



Le labre est conforme à celui des types de *aequatus*. Le VIe article antennaire (Fig. 4A) est plus allongé (L/l = 1,90-2 vs 1,63) et les sensilles sont de longueurs un peu inégales, le postérieur (26,5) entre l'intermédiaire (34) et l'antérieur (23,5). Palpes avec 18-20 sensilles chez les femelles et environ 40 chez les mâles. Le rapport 2ème tarse/griffe en XII est beaucoup plus élevé (11,5 vs 8,3) et surtout la griffe présente un denticule sternal très net à toutes les pattes, comme chez *niveus* (Fig. 4B).

La taille est un peu plus faible que celle du paratype de *aequatus* (2ème tarse XII = 126, 128 vs 147 µm) et la pilosité très légèrement moins fournie.

FIG. 4. — *Lophoturus* cf. *aequatus* Loomis, de Key Largo, Florida. A :: article VI de l'antenne gauche d'un mâle adulte, face tergale. B : tarse XII gauche d'une femelle à 12 pp. a, i, p = sensilles basiconiques antérieur, intermédiaire, postérieur ; c = sensille coeloconique.

FIG. 4. — Lophoturus *cf.* aequatus *Loomis, from Key Largo, Florida. A: left antennal article VI of an adult male, tergal side. B: left tarsus XII of a 12 leg-paired female. a, i, p = anterior, intermediate, posterior basiconic sensilla; c = coeloconic sensillum.*

Le Tableau 2 ci-dessous regroupe quelques valeurs comparatives.

TABLEAU 2. — Caractères morphologiques comparés de trois espèces de *Lophoturus*.
TABLE 2. — Compared morphological features in three Lophoturus *species.*

	Ant. VI, L/l	Ant. VI, sens.	ta XII	ta XIII	Dent griffe
L. niveus	3	inégaux	220 µm	252 µm	+
L. cf. *aequatus*	1,90 - 2	inégaux	126 - 128 µm	135 - 146 µm	+
L. aequatus	1,63	subégaux	147 µm	174 µm	-

CONDÉ & TERVER (1979 : 143) ont cité de Cuba (Jatibonico) des spécimens proches des types de *aequatus* (griffes sans dent, tarse XII : 146 µm). Des Petites Antilles et des Bahamas (Saint-Eustache, New Providence), CONDÉ &TERVER (1965 : 134) ont pu étudier des spécimens pourvus d'une dent plus ou moins marquée aux griffes. Ceux de Saint-Eustache (2 femelles à 13 pp., 1 femelle à 12 pp.), assez grands (ta XIII : 202, 208 µm ; ta XII : 170 µm), avec 22-23 sensilles sur les palpes. Ceux de New Providence (5 mâles, 7 femelles à 13 pp.) sont, comme les types de *niveus*, les plus grands du complexe (ta XIII : 178-240 µm mâles, 222-256 µm femelles) avec 22-29 sensilles sur les palpes des femelles et 41-56 sur ceux des mâles.

Les spécimens de Floride montrent une combinaison de caractères attribués les uns à *L. aequatus* (labre, faibles dimensions), les autres à *L. niveus* (griffes, allongement du tarse), avec aussi des éléments intermédiaires (VIe article de l'antenne). En rapprochant ces spécimens de *L. aequatus*, plutôt que de *L. niveus*, nous privilégions le critère du labre en considérant que l'absence totale d'épines cuticulaires chez *niveus* est un caractère dérivé par rapport à la présence de plusieurs rangées ou d'une seule, comme chez *aequatus*.

Source : MNHN, Paris

RÉFÉRENCES

CONDÉ, B., 1961. — Diplopodes Pénicillates des Açores et de Madère. *Bol. municip. Funchal*, **14** : 7-10.

CONDÉ, B., 1972. — Présence aux Bermudes de Diplopodes Pénicillates et d'Arachnides Palpigrades. *Revue Ecol. Biol. Sol*, **9** : 127-129.

CONDÉ, B. & NGUYEN DUY - JACQUEMIN, M., 1987. — Le statut de *Polyxenus ceylonicus* Pocock et de *Polyxenus poecilus* Chamberlin (Diplopodes Pénicillates). *Revue Ecol. Biol. Sol*, **24** : 99-107.

CONDÉ, B. & NGUYEN DUY - JACQUEMIN, M., 1993. — Parthénogenèse et reproduction bisexuée dans le complexe de *Polyxenus lagurus* (L.). *Biogeographica*, **70 :** 41-48.

CONDÉ, B. & TERVER, D., 1965. — Les Pénicillates de Haïti décrits par H. F. Loomis. *Studies on the Fauna of Curaçao and other Caribbean Islands*, **22** : 124-134.

CONDÉ, B. & TERVER, D., 1979. — Missions Muséum Antilles, Diplopodes Pénicillates. *Revue Ecol. Biol. Sol*, **16** : 137-149.

ISHII, K., 1983. — A new Species of Penicillata Diplopods of the Family Polyxenidae (Diplopoda : Penicillata) from Japan. *Can. Ent.*, **115** : 1355-1357.

ISHII, K. & CHOI, S. S., 1988. — A new Species of the Genus *Polyxenus* (Diplopoda : Penicillata : Polyxenidae) from Korea. *Can. Ent.*, **120** : 711-715.

ISHII, K. & LIANG L., 1990. — Two new Species of Penicillate Diplopods of the Family Polyxenidae (Diplopoda : Penicillata) from China. *Can. Ent.*, **122** : 1239-1246.

NGUYEN DUY - JACQUEMIN, M., 1976. — Etude de la variabilité des caractères de deux espèces du genre *Polyxenus*, *P. lagurus* (L.) et *P. fasciculatus* Say (Diplopode, Pénicillate). *Bull. Mus. natn. Hist. nat., Zool. 249, 3ème Sér.* **356** : 105-118.

NGUYEN DUY - JACQUEMIN, M. & CONDÉ, B.,1984. — Nouvelle description et statut de *Polyxenus bartschi* Chamberlin (Diplopodes Pénicillates). *Bull. Mus. natn. Hist. nat., 4ème Sér., sec. A*, **6** : 721-728.

PIERCE,W. D., 1940. — A rare Myriapod from Anacapa Island compared with two Texas Species. *Bull. South. Calif. Acad. Sci.*, **39** : 158-171.

Source : MNHN, Paris

Source : MNHN, Paris

About the Taxomomy of Spanish Scolopendrellidae

Maria Teresa DOMINGUEZ RODRIGUEZ

Centro de Enseñanza Superior San Pablo C.E.U. Carretera Boadilla del Monte, Km. 5.300
E-28660 Boadilla del Monte, Madrid, Espagne

ABSTRACT

According to the usual morphological characters, Spanish specimens of the family Scolopendrellidae, genus *Scolopendrellopsis*, subgenus *Symphylellopsis*, has been analysed. Those show some mixed characters; for example, it has been found species that show the character "Tömösvary organs with long prolongations" that identified with *Scolopendrellopsis (Symphylellopsis) pauli* n. sp., joined to the character "12 tergal setae on the tergites without posterior prolongations" that belongs to the species *Scolopendrellopsis (Symphylellopsis) selgae* Dominguez. This suggests that the importance of the last character should be decreased.

It has been analysed and discussed the other more important characters that are usually employed in this group of symphylids.

RÉSUMÉ

A propos de la taxinomie des Scolopendrellidae d'Espagne (Symphyla).

Des spécimens espagnols de la famille Scolopendrellidae, du genre *Scolopendrellopsis*, et du sous-genre *Symphylellopsis*, ont été étudiés en accord avec les critères morphologiques usuels. Ils montrent la présence de caractères hybrides : par exemple, on a rencontré des spécimens présentant le caractère "Organes de Tömösvary pourvus de longs prolongements", ce qui caractérise *Scolopendrellopsis (Symphylellopsis) pauli* n. sp., associé au caractère "12 soies tergales sur les tergites dépourvus de prolongations postérieures" qui appartient à l'espèce *Scolopendrellopsis (Symphylellopsis) selgae* Dominguez. Ceci suggère que l'importance accordée à ce dernier critère doit être réduite.

D'autres caractères habituellement employés dans ce groupe de symphyles ont été étudiés et sont discutés.

DOMINGUEZ - RODRIGUEZ, M. T., 1996.— About the taxomomy of Spanish Scolopendrellidae. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 137. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

Source : MNHN, Paris

Some Observations on the Onychophoran Fauna of Tasmania

Hilke RUHBERG * & *Robert* MESIBOV **

* Zoologisches Institut und Zoologisches Museum der Universität Hamburg
Martin-Luther-King-Platz, 3 D- 20146 Hamburg, Germany
** P.O. BOX 700, Burnie, Tasmania, Australia 7320

ABSTRACT

At least nine species of Peripatopsidae (Onychophora) are native to Tasmania. The four currently recognized viviparous species, all endemic, have 15 pairs of legs and are restricted to northeastern or southwestern parts of the main island: *Tasmanipatus anophthalmus* and *T. barretti* are only found in the North East, and two species of a new genus (as yet undescribed) mainly occur in the South West's World Heritage Area (WHA). All other known species are oviparous, have 14 pairs of legs and were previously identified as *Ooperipatellus insignis*, found in Victoria on the Australian mainland. Egg-laying Tasmanian Onychophora are widely distributed and sometimes locally abundant. Taxonomic characters for oviparous species are here reviewed and it is suggested that "*O. insignis*" in Tasmania is in fact a group of endemic species.

RÉSUMÉ

Observations sur la faune des onychophores de Tasmanie.

Neuf espèces au moins de la famille Peripatopsidae (Onychophora) sont originaires de Tasmanie. Les quatre espèces vivipares connues, toutes endémiques, sont munies de 15 paires de pattes ; elles montrent une distribution restreinte : *Tasmanipatus anophthalmus* et *T. barretti* ont été exclusivement trouvées dans le Nord-Ouest et deux espèces d'un nouveau genre (inédit) existent surtout au South-West's World Heritage Area (WHA). Toutes les autres espèces connues sont ovipares et possèdent 14 paires de pattes. On les a regroupées jusqu'à présent sous l'espèce *Ooperipatellus insignis*, trouvée à Victoria sur le continent australien. Les Onychophores ovipares de la Tasmanie présentent une large répartition et abondent parfois en certains endroits. Ce travail propose une révision des caractères taxinomiques et suggère que "*O. insignis*" représente en fait un groupe d'espèces endémiques de Tasmanie.

INTRODUCTION

Onychophora frequently appear in phylogenetic discussions of the Arthropod relationships, and in zoogeographic discussions of the Gondwanan element in fauna of the Southern Hemisphere. Despite the scientific importance of the group onychophoran taxonomy, especially at the species level, is far from satisfactory (RUHBERG, 1992). This is particularly true for the Onychophora of Tasmania. Although the first record of a Tasmanian species was published 100 years ago (SPENCER, 1895), very little collecting and no taxonomic studies were carried out over the following 80 years. A "boom" in Tasmanian onychophoran research began

RUHBERG, H. & MESIBOV, R., 1996. — Some observations on the Onychophoran fauna of Tasmania. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 139-150. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

with a visit to the island by Dr. V. van der LANDE in 1977. The present authors and their colleagues have been studying the Tasmanian fauna since the mid-1980's, and considerable progress has been made towards a comprehensive monograph (RUHBERG & MESIBOV, in prep.).

TASMANIA - A SPECIAL ISLAND

Global climatic changes and other events have resulted in Tasmania being separated from the Australian continent on several occasions during the past 2.5 million years. Australia itself is an isolated remnant of Gondwana and thus is rich in ancient groups of its flora and fauna with high percentage of endemisms (SMITH *et al.*, 1993). Tasmania experienced several highland glaciations during the Pleistocene (DARLINGTON, 1969). The present isolation as an island is believed to have stabilized some 6000 years ago. Cooling factors peculiar to this island together with isolation periods resulted in the evolution of numerous taxa of plants and animals which are now endemic to Tasmania, and has made this island an important repository and refuge for archaic elements of great biological interest and significance. Amongst these are the Onychophora, commonly referred to as "*Peripatus*", "Velvet Worms" or "Living Fossils".

HISTORY OF ONYCHOPHORAN RESEARCH IN TASMANIA

A "rather bleached specimen with fifteen pairs of legs" in the Macleay Museum in Sydney was first noted by FLETCHER (1890) as demonstrating "the occurrence of '*Peripatus Leuckarti*' in Tasmania". Unfortunately this specimen no longer exists in the museum's collections (D.S. HORNING, pers. comm., 1994), and nothing more is known of its morphology or provenance.

Three years later, Sir Baldwin SPENCER collected some 15 specimens of what he called "*Peripatus insignis*" at Dee Bridge in south central Tasmania (SPENCER, 1895). *Peripatus insignis* was the name which had been given by DENDY (1890) to the second only known oviparous onychophoran described from Macedon, Victoria on the Australian mainland. Both the Victorian and Tasmanian specimens had 14 pairs of legs. However, SPENCER (1895) mentioned differences in size between the mainland and the Tasmanian form. DENDY (1900) erected the genus *Ooperipatus* to contain *all* oviparous Australian Onychophora, regardless of whether they had 14 or 15 pairs of legs. In his famous monograph on the oviparous species of Onychophora, he himself laid the foundation for future taxonomic confusion when he synonymized the Victorian *Ooperipatus insignis* from Macedon and the Tasmanian "*insignis*" from Dee Bridge (DENDY, 1902: 403, 408).

A note by BAEHR (1977) on Australian Onychophora included the description of a new species with 14 pairs of legs, *Ooperipatus decoratus*, from Dip Falls in northwestern Tasmania. The type material, thought until recently to be missing, has now been relocated and re-examined by the senior author.

Following a collecting trip to western Tasmania in 1977, Dr. V. van der LANDE requested additional material from Dr. J. HICKMAN of the University of Tasmania, as a form with 15 pairs of legs among her specimens could obviously *not* be identified as *Ooperipatus insignis*. Her request encouraged local zoologists to deliberately search for Onychophora. In 1983, Leigh WINSOR (unpublished report) noted the occurrence of a form with 15 pairs of legs, which he called "*Peripatoides leuckarti*", near the Franklin River in the South-West (MALCOLM, 1987). A second form with 15 pairs of legs from northeastern Tasmania, was found by the junior author in 1984, and was later described as *Tasmanipatus barretti* together with a third species, *Tasmanipatus anophthalmus* by RUHBERG *et al.* (1991). At the same time, in 1984, the senior author was completing a revision of the Peripatopsidae of the world, and had available for study only 18 preserved museum specimens from Tasmania, all of them in rather bad condition. Accordingly the results were tentative and indicated a need for further work on fresh material. RUHBERG (1985) retained the genus name *Ooperipatus* for its generotype *Ooperipatus oviparus*

Source : MNHN, Paris

(a larger oviparous form with 15 pairs of legs from Victoria) and erected a new genus: *Ooperipatellus*, to contain all remaining oviparous species with 14 pairs of legs. She considered the meagre Tasmanian material in hand to be conspecific with two redescribed and renamed species from the Australian mainland: *Euperipatoides leuckarti* (SAENGER, 1869), a viviparous form from New South Wales, with 15 pairs of legs, and *Ooperipatellus insignis* (DENDY, 1890), from Victoria, with 14 pairs of legs.

An Australia-wide survey of Onychophora was begun in 1985 by Drs. N. N. TAIT and D. A. BRISCOE following their discovery of New South Wales forms with peculiar head organs (TAIT & BRISCOE, 1990). In 1987, TAIT & BRISCOE collected Onychophora throughout Tasmania, including remote portions of the World Heritage Area in the South-West. These visits, aimed principally at securing material for allozyme electrophoretic investigations (TAIT & BRISCOE, in SMITH *et al.*, 1993), stimulated the junior author to begin intensive field studies of onychophoran conservation (e.g. MESIBOV, 1988, 1990, 1994). The senior author made the first of three visits to Tasmania in 1989, and Dr. D. ROWELL has included recently collected Tasmanian forms in his studies of chromosomal variation and chromosomal evolution within a sample of Australian Peripatopsidae (ROWELL, unpubl. obs.; ROWELL *et al.*, 1995).

As a result of all these recent activities there is now a rich supply of material available for further taxonomic work on the Peripatopsidae of Tasmania enabling the earlier studies to be reassessed. The first questions to be answered are:

(1) Are the Tasmanian species referred to *Euperipatoides leuckarti* and *Ooperipatellus insignis* conspecific with their mainland counterparts?

and:

(2) Are there more species in Tasmania than at present described?

In what follows, we attempt to answer these questions, concentrating on the taxonomic complexities of the oviparous forms. We begin, however, with a brief review of the viviparous species.

VIVIPAROUS TASMANIAN ONYCHOPHORA

All known viviparous[1] forms from Tasmania have 15 pairs of legs in both sexes. Their distributions are remarkably restricted, with one group found only in the North-East and the other in the South-West (FIG. 1a).

One of the northeastern species, *Tasmanipatus anophthalmus* Ruhberg *et al.*,1991, is white and "blind" (RUHBERG *et al.*, 1991; MESIBOV & RUHBERG, 1991). Its congener, *T. barretti* Ruhberg *et al.*, 1991, has obvious eyes and is dorsally pinkish pigmented. The two species occur parapatrically in forest habitats over ca. 1,000 sq. km. (RUHBERG *et. al.*, 1991; MESIBOV & RUHBERG, 1991). Histological investigations have revealed that an "inner" eye occurs in both species, and that *T. anophthalmus* lacks the lens and the retina-pigment found in this structure in *T. barretti* (RUHBERG *et al.*, in prep.).

Viviparous forms from southwestern Tasmania were previously referred to *Euperipatoides leuckarti* (Saenger, 1869), (RUHBERG, 1985). It now seems clear that the southwestern viviparous Onychophora represent two allopatrically distributed species (FIG. 1a) in a new genus, to be described in a forthcoming paper (RUHBERG, in prep.).

In summary, there is now strong evidence from morphological and phylogenetic studies (RUHBERG in prep.; REID, 1995, in prep.), chromosome studies (ROWELL *et al.*, 1995) and allozyme investigations (TAIT & BRISCOE in: SMITH *et al.*, 1993), that *none* of the Tasmanian

---

1 *All* viviparous Peripatopsidae from Australia are new considered to be ovoviviparous (CAMPIGLIA & WALKER, 1995; REID, pers. comm.).

Source : MNHN, Paris

viviparous species are conspecific, or even congeneric, with mainland Australian forms. All show clear-cut diagnostic features and are further characterized by their geographically restricted distributions.

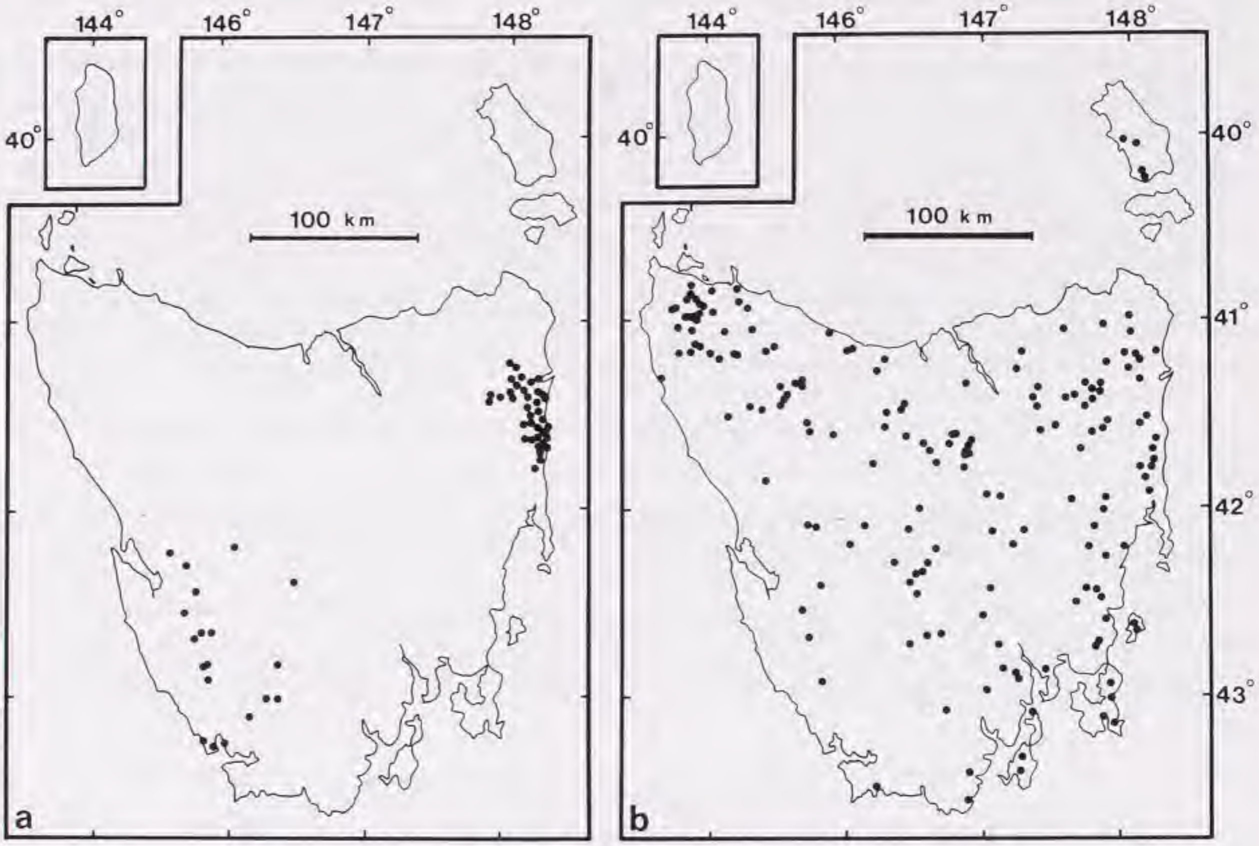


FIG. 1 a-b. — Distribution of (a) viviparous and of (b) oviparous Peripatopsidae in Tasmania.

OVIPAROUS TASMANIAN ONYCHOPHORA

Oviparous forms were previously identified with the Victorian *Ooperipatellus insignis* (DENDY, 1890), (RUHBERG, 1985). Egg-layers are found throughout the main island of Tasmania and on several offshore islands (Fig. 1b). They occur in forest, woodland and scrub habitats from sea level to at least 1,100 m and are sometimes locally abundant. Occurrences in forest after clearfell logging, part-clearing or burning demonstrate that oviparous species, at least in the short term, are remarkably tolerant of habitat disturbance (MESIBOV, unpubl. results).

In contrast to viviparous species in Tasmania, oviparous forms are superficially very similar. All females have a prominent ovipositor and lay shelled eggs (Figs 4e, 3d), all males have a nearly uniform distribution-pattern of crural papillae on leg-pairs 6-13, and both sexes have 14 pairs of walking appendages. These characters are shared by Victorian and New Zealand oviparous species within the genus *Ooperipatellus* which are also alike in having a 2n chromosome number of 42. In contrast there is much variation within the viviparous forms. *Tasmanipatus*- spp. have 2n = 34 or 36 and the yet undescribed viviparous southwestern genus has 2n = 18, with interspecific variation in sex chromosomes (ROWELL *et al.*, 1995).

Early taxonomic studies relied to a large extent upon colour and colour-pattern, as can be seen in DENDY's impressive opus "On the oviparous species of Onychophora" (DENDY, 1902;

Source : MNHN, Paris

pl. 19, Figs 1-3). We have found that colour and colour-pattern *per se* are unreliable characters in onychophoran systematics, and that other traits need to be examined (RUHBERG, 1992).

In an effort to improve the taxonomy of oviparous onychophorans, and to arrive at a well grounded biospecies-concept, the present authors, in collaboration with specialists, are using data on external and internal anatomy, histology and ultrastructure, allozyme electrophoresis, behaviour and distribution patterns. Specimens for these investigations derive almost entirely from our own field collections (mainly deposited in the Queen Victoria Museum and Art Gallery, Launceston, Tasmania), and include animals bred in the laboratory by H. R. in Hamburg. The results of particular studies will be published in forthcoming papers. Here we review progress in identifying species–diagnostic characters.

DIAGNOSTIC CHARACTER VARIATIONS IN OVIPAROUS ONYCHOPHORA

For the sake of completeness we begin with a revision of the genus *Ooperipatellus.*

Ooperipatellus s. str. Ruhberg, 1985.

Type species: *Peripatus insignis* Dendy, 1890 from Macedon, Victoria (to be redescribed in REID, in prep.).

Distribution

Victoria, Tasmania, New Zealand.

Diagnosis

Ooperipatellus is a genus of Australasian oviparous peripatopsid Onychophora with 14 pairs of legs. Females have a prominent ovipositor and lay shelled eggs, males have crural papillae on leg pairs 6-13. Outer jaw blade without accessory tooth.

Differential diagnosis

Ooperipatellus, s. str., is distinguished from all other known oviparous peripatopsid genera on the basis of a unique combination of characters (for comparison see RUHBERG, 1985). It is distinguished from *Ooperipatus,* the "larger Victorian genus" which has 15 pairs of legs, male crural papillae on leg pairs 2-14, and an accessory tooth on the outer jaw blade.

Ooperipatellus is separable from most other currently recognized, but as yet undescribed oviparous mainland Australian species (REID, in prep.), in lacking characteristic head organs. Further the latter forms show different patterns of male crural papillae.

Ooperipatellus nanus Ruhberg, 1985, a tiny form from southern New Zealand, with only 13 pairs of legs, which was previously tentatively assigned to this genus (RUHBERG, 1985: 131) shows more unique characters in adults now than could be deduced from juveniles at hand in 1985. This species has to be transferred to a new genus (RUHBERG, in prep.).

Description

Oviparous peripatopsids. Leg number constant within species, last leg pair well developed, with claws. Foot with 3 distal papillae, no basal papillae. Anal cone of variable length (Fig. 2f, 4a-c). Genital pore in males of variable shape (Figs 4a-c), females with distinct ovipositor of variable length (Fig. 4e).

Males with accessory glands coiled around each other.

Females with paired, flat ovaries, closely attached to the pericardial septum. Ovarial eggs exogeneous and highly variable in size; rudiments of receptacula seminis only present in juvenile females, lost in adults. Additional pouches lacking. Uterine eggs of varying developmental stages.

Source : MNHN, Paris

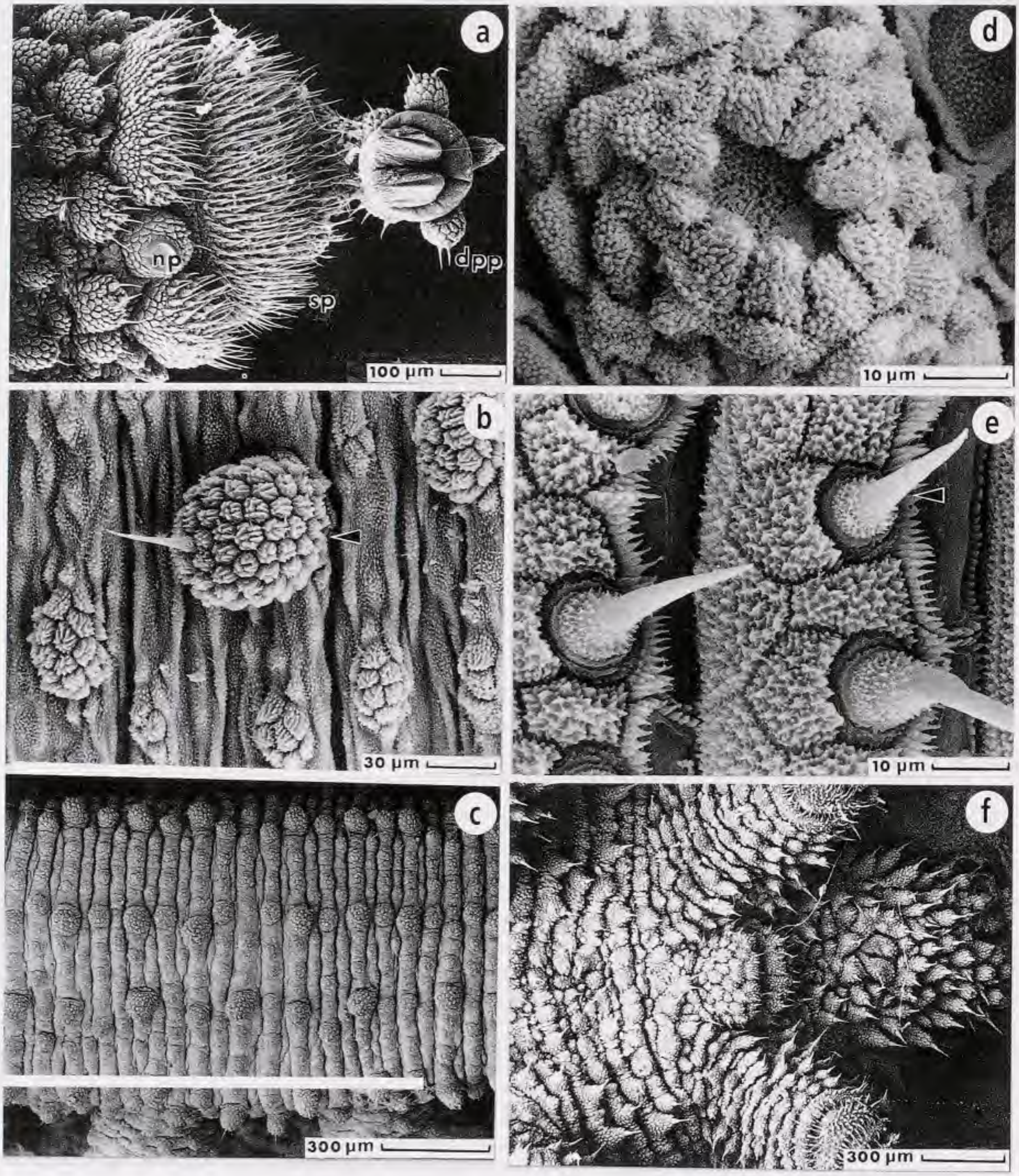


FIG. 2 a-f. — SEMs of Tasmanian Onychophora: (a) Fourth foot with three distal papillae (dpp), nephropore (np) and spinous pads (sp); (b) Dorsal skin with primary (arrowhead) and secondary dermal papillae (a-b, e: *Ooperipatellus* sp. from Black River); (c) Typical pattern of dermal papillae and plical folds in *O. decoratus* ; (d) Yet undescribed structure on dorsolateral skin in *Ooperipatellus* sp. from Christmas Hill; (e) Antennal tip: second and third annulus, each with one row of mechanoreceptors only (arrowhead); (f) *Tasmanipatus barretti*: Hind end of body with a pronounced anal cone.

Source : MNHN, Paris

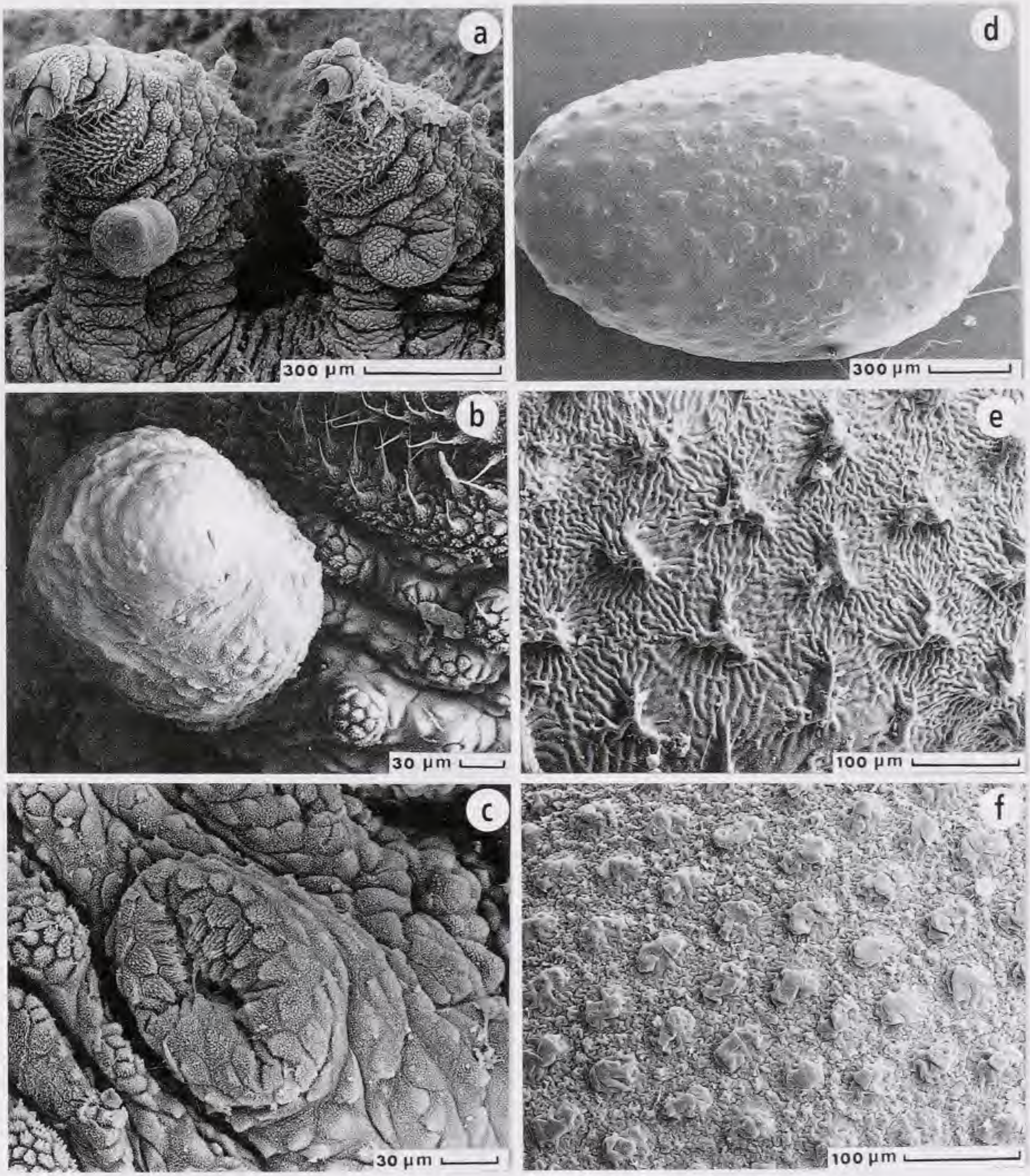


FIG. 3 a-f. — SEMs: (a-b) Different size and shape of male crural papillae in *Ooperipatellus* sp. from Black River: (a) 11th (left on FIG.) and 12th leg (right on FIG.); (b) 7th leg; (c) Crural papilla on 12th leg in *O. decoratus*; (d-f) Chorion of ripe eggs: (d) Egg from a yet undescribed oviparous species from Bellenden Ker, N- Queensland; (e) Sculpture of egg-chorion in *O. decoratus* ; (f) egg-chorion in *Ooperipatus oviparus* from Victoria.

Source : MNHN, Paris

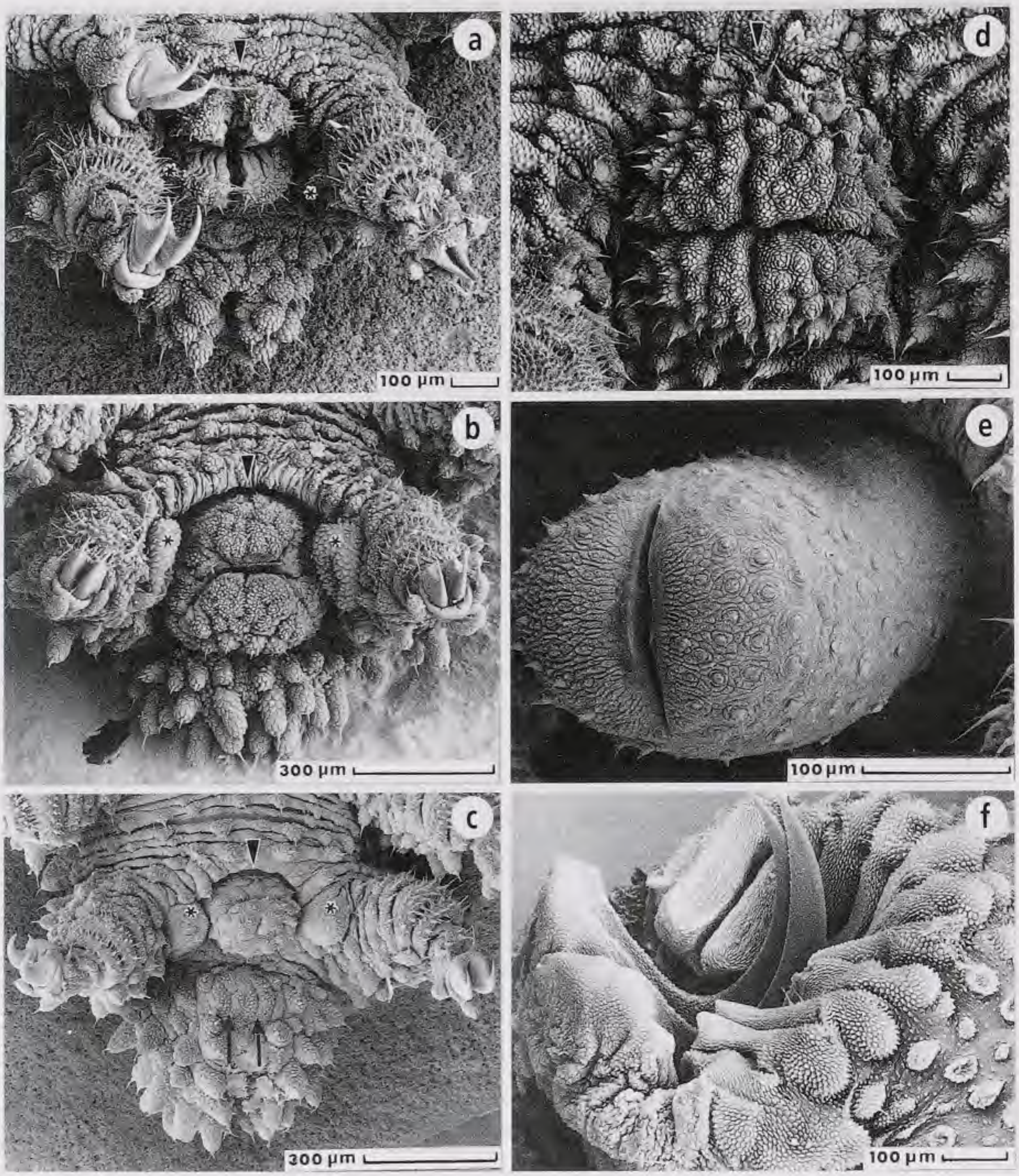


FIG. 4 a-f. — SEMs: (a-c) Different shape and size of genital pores (arrowheads), crural papillae of last legs (asterisks) and anal-slits (arrows) within male oviparous species; (a) Body's hind end in a sexual active *O. decoratus*, collected by R. M. during a "swarming night" in October 1992; (b) *Ooperipatellus* sp. from Black River, Tasmania; (c) *Ooperipatus oviparus* from Victoria; (d) Cruciform male genital pore in the viviparous *Tasmanipatus barretti* ; (e) Ovipositor of *O. decoratus* ; (f) Distinct head organ in a yet undescribed viviparous species from the Tinderry Mts., NSW (lateral view).

Source : MNHN, Paris

Species–diagnostic characters so far recognized in *Ooperipatellus*, are noted below:

External Anatomy; Internal Anatomy; Histology and Ultrastructure; Allozyme Electrophoresis; Behaviour; Distribution; Other Characters.

a) External Anatomy

The number, size, shape and pigmentation of spinous pads of the foot; the position of the nephropore on the 4th and 5th pair of legs; the number, size and arrangement of distal and basal foot papillae (Fig. 2a); the structure and distribution of dorsal skin papillae (Figs 2b-c), the number of dorsal plical folds (Fig. 2c), the presence or absence of as yet undescribed structures on the latero-dorsal surface (Fig. 2d); the size of the primary dorsal papillae (Figs 2b-c), which varies to give an overall "smooth" or "warty" appearance to the body; the number of rows of mechanoreceptors on the second and third distal annulus of the antenna (Fig. 2e); the presence or absence of a deep wrinkle at the antennal base (TAIT & BRISCOE, 1987); the size, shape and position of the male crural papillae on leg-pairs 6-13 (Figs 3a-c, 4a-c), the degree of elongation of the anal cone (Fig. 2f), the degree of reduction of the last legs; and the overall size, e.g. the "stoutness" or the "slenderness" of the body (cf. BOUVIER, 1905; pl. I, Figs 4 & 6).

Coloration characters must be used with care. Even when very distinctive *dorsal* patterns appear in a population (e.g. a "striped", "chequered", "diamond", "chessboard", "spotted", or "speckled" pattern) there can be substantial within-population variation (BROCKMANN, 1994; Figs 7-8). Eye coloration is an unreliable character, it seems to change in fixative. Nevertheless, antennae appear to have species-characteristic patterns of annular coloration which are already visible in late embryos (BROCKMANN, 1994). The occurrence or absence of pigment and/or colour patterns of the *ventral* body surface is characteristic as well and so is the pigmentation of the hatchling in oviparous respectively of the newborn in viviparous species (RUHBERG, pers. observations).

b) Internal Anatomy

Among the anatomical characters are mainly the peculiarities of the genital tracts in both sexes. In *Ooperipatellus*, species can be distinguished by the following characters: the position and shape of male crural glands (within the leg or free in the body cavity) and anal glands (e.g. accessory glands coiled or uncoiled). The structure and development of the ovarial and uterine eggs in the females vary in number and age.

c) Histology and Ultrastructure (SEM, TEM)

The sculpture of the chorion of the ripe uterine or freshly deposited egg (DENDY, 1902; pl. 21; Figs 20-27, and this report, Figs 3d-f) is highly characteristic. Of further taxonomic value are SEM-details of the integument, including the size, shape and number of scales on the main dorsal papillae (Fig. 2b); features of the head, feet and genital region, and as yet undescribed structures in certain species (Fig. 2d) which are currently under investigation with regard to their function and taxonomic value (RUHBERG, in prep.).

First results from histological studies of *O. decoratus* (males, females and eggs) are promising (BROCKMANN, 1994), in that this species shows clear histological differences when compared with *O. insignis*, as described by DENDY (1902). Unfortunately, freshly killed material is needed for such studies and histological characters may not be of use in identifying museum specimens. The same caution applies to use of ultrastructural differences noted in examination of fresh *O. decoratus* and *O. viridimaculatus* (DENDY, 1900; RUHBERG & BROCKMANN, in prep.); among the most valuable TEM-criteria are details of the spermatophores. In contrast, SEM-investigations are possible with old museum material as well (RUHBERG, 1985, 1992).

d) Allozyme Electrophoresis

Characteristic allozyme patterns in Tasmanian oviparous forms have been used by TAIT & BRISCOE (in: SMITH *et al.*, 1993) as the basis for separating taxa in the "*O. insignis*" complex. These "electrotaxa" are tentative, but the patterns suggest, that oviparous forms can have

Source : MNHN, Paris

restricted distributions within Tasmania, and that the Tasmanian forms are only distantly related to oviparous Onychophora on the Australian mainland.

e) Behaviour

Ooperipatellus viridimaculatus from Shennandoah Saddle, New Zealand, South Island, lies still when picked up and is remarkably sluggish in culture (RUHBERG, pers. obs.), while a new *Ooperipatellus* -species from northwest Tasmania (RUHBERG & MESIBOV, in prep.) very rapidly coils itself into a tight helix when disturbed. *O. viridimaculatus* is also unusual in carrying its antennae mostly bent backwards. A curious "swarming" of *O. decoratus* was noted one night in October 1992, when hundreds of individuals were seen climbing trees about an hour after sunset at a field site in northwest Tasmania (MESIBOV, unpubl. obs.). A random sample from the swarm proved to be 90% males, with individuals showing widely opened genital pores (FIG. 4a), and drops and threads of secretion clinging to crural gland openings (RUHBERG, unpubl. obs.). It is not yet known whether any other *Ooperipatellus* species exhibit swarming.

f) Distribution

Onychophoran populations are generally rather small and their distribution is disjunct on both large and small scales. In several places egg-layers occur sympatrically with live–bearers. Within Tasmanian Onychophora all possible distributional patterns do occur: broad sympatry, narrow sympatry, parapatry and allopatry (MESIBOV, unpubl. obs.). A few species seem to be better dispersers than others (e.g. *T. barretti* compared to *T. anophthalmus*). Onychophora in the State have been collected in almost all forest types: dry, wet and alpine. Although oviparous Onychophora are almost ubiquitous in Tasmania (Fig. 1b), it is clear from our preliminary taxonomic work that individual species can be restricted to relatively small areas. It seems unlikely that differing habitat preferences account for range limitation, and in all cases the microclimate parameters are similar in the prefered shelters: under logs and stones, in leaf litter and soil crevices. Distribution limits may be "historically" determined or may be controlled by interactions with other Onychophora, as is suspected to be the case for the parapatric *Tasmanipatus* species of northeast Tasmania (MESIBOV & RUHBERG, 1991). Where range boundaries are sharp, location may be used as a species-diagnostic character.

g) Other Characters

There is potential for using secretions as species-diagnostic biochemical characters. Recently ELIOTT *et al.* (1993) have shown that crural gland secretion in males of the viviparous *Cephalofovea tomahmontis* Ruhberg *et al.*, 1988, acts as a chemoattractant for conspecific females. Extensions of this study to oviparous species may reveal a range of biochemically distinctive, pheromonal attractants. Onychophoran slime may also be taxonomically useful (RENWRANTZ & RUHBERG, in prep.), although the slimes of the *Ooperipatellus*-species so far studied appear to be nearly indistinguishable. Chromosome studies also have so far documented the close relationship of *Ooperipatellus*-species from Tasmania, Victoria and New Zealand (ROWELL, pers. comm.). Onychophora have the right properties (small, isolated populations) for the study of chromosome driven speciation. As has been outlined before there is much variation in the chromosome numbers within the Australian viviparous forms while all oviparous representatives of *Ooperipatellus* investigated are alike in having a 2n = 42 chromosome-number-pattern (ROWELL *et al.*, 1995, in press). The latter is also the largest chromosome number observed to date in Onychophora.

DISCUSSION

Returning to our earlier questions, we are now confident on the basis of morphological and other studies that (1) neither *Euperipatoides leuckarti* nor *Ooperipatellus insignis* is present in Tasmania, and (2) that Tasmania is home to four, not three, viviparous species and to at least five, not one, oviparous species of Onychophora. The oviparous species have congeneric

Source : MNHN, Paris

relatives in Victoria and New Zealand and will be described in forthcoming papers (RUHBERG & MESIBOV, in prep.).

For identification in the field it is convenient that viviparous Tasmanian species all have 15 pairs of legs, while oviparous Tasmanian species all have 14 pairs of legs. Identifications within the taxonomically difficult oviparous group will depend on careful examination of many of the subtle characters noted in this paper, a procedure made more difficult by the absence in the Tasmanian forms of "complicated characters" sensu HENNIG, such as the head organs (Fig. 4f) found in some oviparous and viviparous Onychophora on the Australian mainland (RUHBERG *et al.*, 1988; TAIT & BRISCOE, 1990; REID, in prep.).

Phylogenetic studies of oviparous forms will also be difficult, and a combined morphological, genetic and ecological approach will be the key to understanding their radiation within Australia. The effort will be worthwhile, as it will shed light on whether egg-laying or (ovo-)viviparity is the primitive reproductive mode in the peripatopsid Onychophora. The co-existence of both reproductive modes in Tasmania is both a mystery and an opportunity for understanding the respective advantages of the two strategies.

ACKNOWLEDGEMENTS

The authors are grateful for financial support from the following sources: (to H.R.) the Deutsche Forschungsgemeinschaft; grants DFG Ru: 358/1-5 and 2-1; (to R.M.) the Plomley Foundation (through the Queen Victoria Museum and Art Gallery, Launceston), and the Australian Heritage Commission (through the Tasmanian Department of Lands, Parks and Wildlife). For the loan of museum specimens H.R. is indepted to Dr. T. KINGSTON, Curator of Zoology at the QVMAG, Dr. R. RAVEN, Senior Curator of Chelicerata at the Queensland Museum, South Brisbane, Dr. P. M. JOHNS, Canterbury University, Christchurch, N. Z., Dr. D. BURCKHARDT, collections for the Muséum d'Histoire naturelle, Genève, and Mr. P. P. PARILLO, Division of Insects , Field Museum of Natural History, Chicago, Illinois.

For skillful technical assistance at the Scanning Electron Microscope we would like to thank Mrs. R. WALTER, Zoology Dept., University of Hamburg. For unpublished notes, records and additional material both authors thank Drs. D. ROWELL and A. REID (Canberra), N. N. TAIT and D. A. BRISCOE (Sydney) and V. v. d. LANDE (Nottingham). Dr. M. H. WALKER (Leicester) kindly corrected H. RUHBERG's original text version.

REFERENCES

BAEHR, M., 1977. — Über einige Onychophoren aus Australien und Tasmanien mit Beschreibung einer neuen Art und Anmerkungen zur Stellung von *Ooperipatus paradoxus* Bouvier, 1915. *Zool. Jb. Syst.*, **104** : 9-19.

BOUVIER, E. L., 1905. — Monographie des Onychophores. *Annls. Sci. nat. (Zool.)*, **2** : 1-383.

BROCKMANN, C., 1994. — Zur Eidonomie, Anatomie und Entwicklungsbiologie von *Ooperipatellus decoratus* (BAEHR, 1977) (Peripatopsidae, Onychophora). *Diplomarbeit des Fachbereiches Biologie der Universität Hamburg* (unveröffentlicht) : 1-102.

CAMPIGLIA, S. S. & WALKER, M. H., 1995. — Developing embryo and cycling changes in the uterus of *Peripatus (Macroperipatus) acacioi* (Onychophora, Peripatidae). *J. Morph.*, **224** : 179-198.

DARLINGTON , P. J., 1969. — Biogeography of the Southern End of the World. *Harvard University Press* (2nd Ed.) :1-236.

DENDY, A., 1890. — Preliminary Account of a New Australian *Peripatus*. *Vict. Naturalist* , **6** : 173.

DENDY, A., 1900. — Preliminary Note on a proposed New Genus of Onychophora. *Zool. Anz.*, **23** : 510.

DENDY, A., 1902. — On the Oviparous Species of Onychophora. *Q. Jl. Micr. Sci.*, **45** : 363-413.

ELIOTT, S., TAIT, N. N. & BRISCOE, D. A., 1993. — A pheromonal function for the crural glands of the Onychophoran *Cephalofovea tomahmontis* (Onychophora: Peripatopsidae). *J. Zool., Lond.*, **231** : 1-9.

FLETCHER, J. J., 1890. — Additional Notes on *Peripatus Leuckarti*. *Proc. Linn. Soc. NSW* (2) **V** (Dec.16) : 469-486.

MALCOLM, H. E., 1987. — Invertebrate Fauna of the Franklin River Area, Tasmania. Report on the Australian and New Zealand Scientific Exploration Society (ANZSES) expedition 1983. *The Tasmanian Naturalist.*, **91** : 5-6.

MESIBOV, R., 1988. — Tasmanian Onychophora. *Unpubl. Report for the Dept. of Lands, Parks and Wildlife, Tasmania* : 1- 44.

MESIBOV, R., 1990. — Velvet Worms: A Special Case of Invertebrate Fauna Conservation. *Tasforests July* **1990** : 53-56.

MESIBOV, R., 1994. — Faunal breaks in Tasmania and their significance for invertebrate conservation. *Mem. Qld. Mus.*, **36** : 133-136.

Source : MNHN, Paris

MESIBOV, R. & RUHBERG, H., 1991. — Ecology and conservation of *Tasmanipatus barretti* and *T. anophthalmus*, parapatric onychophorans (Onychophora: Peripatopsidae) from northeastern Tasmania. *Pap. Proc. Roy. Soc., Tasmania* , **125** : 11-16.

REID, A. L., 1995. — A systematic review of the Peripatopsidae (Onychophora) in Australia. Thesis, North Ride, N. S. W., Macquarie University (unpublished).

ROWELL, D. M., HIGGINS, A. V., BRISCOE, D. A. & TAIT, N. N., 1995. — The use of chromosomal data in the systematics of viviparous onychophorans from Australia (Onychophora: Peripatopsidae). *Zool. J. Linn. Soc.*, **114** : 139-153.

RUHBERG, H., 1985. — Die Peripatopsidae (Onychophora). Systematik, Ökologie, Chorologie und phylogenetische Aspekte. *Zoologica*, **137** : 1-183.

RUHBERG, H., 1992. — "*Peripatus* " – an Approach towards a Modern Monograph. *Ber. nat.-med. Verein Innsbruck*, Suppl. **10** : 441-458.

RUHBERG, H., TAIT, N. N., BRISCOE, D. A. & STORCH, V., 1988. — *Cephalofovea tomahmontis* n. gen., n. sp., an Australian Peripatopsid (Onychophora) with a Unique Cephalic Pit. *Zool. Anz.*, **221** : 117-133.

RUHBERG, H., MESIBOV, R., BRISCOE, D. A. & TAIT, N. N., 1991. — *Tasmanipatus barretti* gen. nov., sp. nov. and *T. anophthalmus* sp. nov.: two new and unusual onychophorans (Onychophora: Peripatopsidae) from northeastern Tasmania. *Pap. Proc. R. Soc. Tasm.*, **125** : 11-16.

SAENGER, H., 1869. — *Peripatus capensis* Sr. et *Peripatus Leuckartii* n. sp. (en russe). *Trav. 2. Congr. nat. russ. Moscou* : 239-262. (Traduit par BOUVIER, E. L., 1901.– A propos d'un travail de H. Saenger sur les Péripates. *Bull. Soc. philom. Paris* **3** : 9-36, pl. : 12-13.

SMITH, S. J., 1993. — Tasmanian Wilderness (Chapter 15) – *In* : S. J. SMITH & M. R. BANKS, *Tasmanian Wilderness – World Heritage Values. Pap. Proc. Roy. Soc. Tasmania*, Hobart : 129-143.

SPENCER, W. B., 1895. — Note on the presence of *Peripatus insignis* in Tasmania. *Proc. R. Soc. Vict.*, **7** : 31-32.

TAIT, N. N. & BRISCOE, D. A., 1987. — *Onychophora in Tasmania*. Unpublished Report on WHA Directed Research Contract : 4 pp + Appendix 5pp.

TAIT., N. N. & BRISCOE, D. A., 1990. — Sexual head structures in the Onychophora: unique modifications for sperm transfer. *J. nat. Hist.*, **24** : 1517-1527.

TAIT, N. N. & BRISCOE, D. A., 1993. — *Peripatus* or Velvet Worms – a contribution to chapter 13. *In* : Threatened, rare and localised plants and animals (by S. J. SMITH & L. GILFEDDER). *In* : S. J. SMITH & M. R. BANKS, *Tasmanian Wilderness – World Heritage Values. Pap. Proc. Roy. Soc. Tasmania*, Hobart : 136-138.

WINSOR, L., 1983. — Onychophorans (Arthropoda: Onychophora) from the Franklin River Area, South Western Tasmania. Unpubl. report on a collection made by the ANZSES Expedition, 1983, 4 pp.

Source : MNHN, Paris

Millipedes as Aids for the Reconstruction of Glacial Refugia (Myriapoda: Diplopoda)

Jörg SPELDA

University of Hohenheim, Institute for Zoology, Garbenstrasse 30, D-70593 Stuttgart, Germany

ABSTRACT

This paper shows that we can discover Quaternary refugia by studying the present distribution of millipedes. Four preconditions are proposed that should be performed by a species used for the reconstruction of a refuge. It should have a low tendency of outspreading, it should be an endemic species, it should be easy to catch and its statements should be supported by other groups of organisms. Concerning two sites at the northern border of the Alps (in the vicinity of Basel/Switzerland and Salzburg/Austria) it is shown that some species of chordeumatids fulfill these conditions. The possibility of speciation after the Ice Age, the character of natural borders, the influence of extinction and men are discussed.

RÉSUMÉ

Utilisation des diplopodes dans la reconstitution des refuges glaciaires.

Ce travail montre qu'il est possible de découvrir des refuges quaternaires en étudiant la répartition actuelle des diplopodes. Quatre conditions préalables sont proposées, qu'une espèce doit remplir afin de pouvoir être utile à la reconstitution d'un refuge glaciaire. Elle doit présenter une faible tendance à la dispersion, être endémique, être facile à capturer et son statut doit être appuyé par d'autres groupes d'organismes. Il est montré que, dans deux sites de la bordure nord des Alpes (près de Bâle, en Suisse et près de Salzbourg, en Autriche), certaines espèces de chordeumatides réunissent ces conditions. La possibilité d'une spéciation post-glaciaire, les caractéristiques des frontières naturelles, l'influence des extinctions et celle de l'homme sont discutées.

INTRODUCTION

The idea of using the present distribution of animals for the reconstruction of glacial refugia has been born at the beginning of our century and is connected with the name of HOLDHAUS (1954), who investigated large parts of the eastern Alps. This research caused a dispute with JANETSCHEK (1956), the other one working on this subject. The main contradiction between them was the existence of inneralpine refugia (as JANETSCHEK stressed) against secondary immigration into those parts (HOLDHAUS' argumentation), however both principally agreed in the existence of glacial refugia in the Alps. HOLDHAUS (1954) mainly investigated beetles (especially wingless ground-beetles and weevils) while JANETSCHEK (1956) based his argumentation on a larger number of taxa. But even earlier the great german myriapodologist VERHOEFF (1917) recognized the importance of millipedes on this subject. He discovered the endemic species in the southern Black Forest and during many excursions in the Alps he

SPELDA, J., 1996. — Millipedes as aids for the reconstruction of glacial refugia (Myriapoda: Diplopoda). *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 151-161. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

improved our knowledge on the distribution of these animals. A lot of his publications deal with the zoogeography of millipedes and he always tried to give explanations of their distribution, summarized in VERHOEFF (1938a).

MATERIAL AND METHODS

Beside the critical evaluation of the older (e.g. ATTEMS, 1949, BIGLER, 1913) and recent literature (e.g. SPELDA, 1991; PEDROLI-CHRISTEN, 1993), many collections have been made by the author since 1988 in southwestern Germany and in the northern Alps.

FAUNISTIC RESULTS

The following records have been unpublished up to now. Making localisation easier for subsequent workers the degrees of longitude and latitude are given for each locality. The sex of the specimens is represented by the scheme (males/females). Collectors are only listed if not identical with the author.

Abbreviations:

Xylvom = *Xylophageuma vomrathi* Verhoeff, 1911; Haanor = *Haasea norica* (Verhoeff, 1913); Hapocu = *Haplogona oculodistincta* (Verhoeff, 1893); Synace = *Syngonopodium aceris* Verhoeff, 1913; Pyrtit = *Pyrgocyphosoma titianum* (Verhoeff, 1910); Liscer = *Listrocheiritium cervinum* Verhoeff, 1925; Lisnor = *Listrocheiritium noricum* Verhoeff, 1913; Lissep = *Listrocheiritium septentrionale* Gulicka, 1965; Rhyale = *Rhymogona alemannica* (Verhoeff, 1910); Rhycer = *Rhymogona cervina* (Verhoeff, 1910); Rhyser = *Rhymogona serrata* (Bigler, 1912); Rhyver = *Rhymogona verhoeffi* (Bigler, 1913); Rhyweh = *Rhymogona wehrana* (Verhoeff, 1910); Rhy = *Rhymogona sp.*

A = Austria; **CH** = Switzerland; **D** = Germany.

CH: Aargau, 2 km ESE Sisseln (08°00'E, 47°33'N), 09.10.1991: Rhy (0/2); **A**: summit of the mountain Gaißberg (13°06'E, 47°48'N), 17.10.1991: Haanor (2/5); Lisnor (3/4); **A**: 1.5 km SW Scharfling at lake Mondsee (13°23'E, 47°47'N), 17.10.1991: Hapocu (3/3, *first record in the northern Alps* !); Synace (3/2); Lisnor (4/3); **A**: highway station "Tauernalm" (13°25'E, 47°15'N), 18.10.1991: Liscer (2/1); **A**: 3 km SSW Rossatz (15°30'E, 48°22'N), 21.10.1991: Lissep (3/1, *first record for Austria*); **CH**: Aargau, 1 km NW Sulz (08°05'E, 47°32'N), 27.10.1991: Rhy (0/6); **CH**: Aargau, 1.5 km SW Eiken (07°59'E, 47°31'N), 27.10.1991: Rhycer (2/1); **D**: 1 km N Hasel near Wehr (07°53'E, 47°39'N), 30.10.1991: Xylvom (4/1); Rhyweh (9/15); Pyrtit (3/1); **D**: 1.5 km SO Inzlingen (07°42'E, 47°34'N), 30.10.1991: Rhyser (10/8); **D**: N Maulburg (07°46'E, 47°39'N), 30.10.1991: Rhyale (3/1); **D**: 1 km S Schallsingen (07°39'E, 47°45'N), 30.10.1991: Rhy (0/6); **D**: 1 km ESE Wittlingen near Lörrach (07°40'E, 47°439N), 30.10.1991: Rhy (0/1); **D**: 1 km NE Neckarhausen (08°39'E, 48°24'N), 01.11.1991: Rhy (0/1); **D**: 1 km E Marbach near Villingen (08°29'E, 48°01'N), 01.11.1991: Rhy (0/3); **D**: Obergießhof, 4.5 km S Hornberg (08°13'E, 48°10'N), 01.11.1991: Rhyver (1/2); **D**: Niedergieß, 3.5 km SSW Hornberg (08°12'E, 48°11'N), 01.11.1991: Xylvom (1/1); Rhyver (2/1); **D**: 1 km NW Hirschsprung, Höllental near Freiburg (08°01'E, 47°56'N), 01.11.1991: Pyrtit (1/0); **D**: 1 km SE Sulzburg (07°43'E, 47°50'N), 18.10.1992: Pyrtit (3/3); Rhy (0/2); **D**: E of Lörrach-Brombach (07°42'E, 47°38'N): Rhyser (2/4); **D**: quarry 1 km E Gerhausen (09°49'E, 48°23'N), pitfall trap, 17.09.-01.10.1992, leg. J. BÖHMER: Rhycer (1/0); **D**: Scheibenfelsen SE Häusern (08°10'E, 47°44'N), pitfall trap, 12.1988.-05.1989, leg. R. MOLENDA: Rhyweh (1/0); **D**: Präg 6 km SSE Todtnau (07°57'E, 47°46'N), pitfall trap, 10.1991, leg. R. MOLENDA: Pyrtit (5/8); **D**: S Badenweiler (07°40'E, 47°47'N), 07.10.1986, leg. A. PEDROLI-CHRISTEN: Pyrtit (0/1); **D**: S Hierbach (08°05'E, 47°40'N), 08.10.1986, leg. A. PEDROLI-CHRISTEN: Pyrtit (0/1); **D**: 1 km SW Altglashütten (08°05'E, 47°51'N), 30.09.1990, leg. A. PEDROLI-CHRISTEN: Pyrtit (1/0).

Source : MNHN, Paris

DISCUSSION AND FURTHER RESULTS

A. Conditions for the use of a species as an aid for the reconstruction of glacial refugia

The use of the present distribution of organisms for the reconstruction of glacial refugia is based on the assumption that it mainly is a consequence of the depauperation during the Ice Age. The main argument for this is, that neither petrophilous (meaning restricted to rocky areas) nor endemic animals occur in Scandinava (HOLDHAUS, 1954; VERHOEFF, 1938a), although we have similar climatic conditions than in the Alps. As Scandinavia was totally covered with an ice-shield during the glaciated periods (NORDAL, 1987) we have a very good explanation for this fact.

To increase the suitability of the used organisms and consequently the validity of their distribution for our purpose, the following conditions should be performed:

A. 1. Low tendency of spreading out

This is of course very important, because there might have been many species that have survived at the refugia. But if they largely spread out after the climate had changed to better conditions their vestiges got lost. Only the few species, that did stay nearby their former refugia, will show us where they have been situated. In some cases the present distribution indicates a north-alpine persistance (e.g. in the beetle *Trechus glacialis*) but it cannot be proved where this species has survived and whether it had a monocentric or polycentric refuge. Automatically this means the more restricted a species is, the better it is suitable for the reconstruction of glacial refugia.

A. 2. Speciation

Endemic species will provide a stronger argument for a refuge than isolated populations of a wider distributed species (but also see below under C. 3.). Without knowing of possible vectors, we simply cannot decide whether there had been a polycentric refuge including several nunataks or massifs de refuge or if the species has obtained parts of its present distribution in more recent times.

Of course we have to ask the question why speciation should take place in the small, isolated populations on their refugia. Referring to this, the theory of "sexual selection by female choice" (EBERHARD, 1985), is of importance. Using its arguments we might suppose that in a small area with a low amount of natural resources (food, hiding-places, etc.) there must be an intensive struggle between the males about the females. These favour males on the base of their genitalia, so that we have a strong selective pressure to surpass the competition. As the direction of this evolutionary process is of random, different populations will go different ways. The smaller a population is, the faster this process will go on.

At smaller refugial areas or at the border of larger ones, suitable places for the survival will be intermitted by hostile areas, e.g. ice streams. As a result of this partition we will probably find a complex of sibling species or subspecies at such places that furnish proof for this.

A. 3. Easy to catch

This condition is of practical value for the researcher and certainly depends on his experience. But there are some species that live at inaccessible places or occur in so low numbers that they will be found only by chance. We know of many species that have been described as being endemic and have later been found elsewhere. Good examples are subterranean species, especially the phreatic species that live in small crevices deep inside the rocks, where equal climatic conditions occur. Most of them have been described as cave species, simply because caves are the only places where men and phreatic species can meet.

Source : MNHN, Paris

A. 4. Confirmation by other organisms

If we do not assume that the outlasting was only a special case in one species or genus, we might expect that endemism may also occur at other groups. This means, the more endemic species from different groups (millipedes, beetles, earthworms, etc.) occur, the better a possible refuge is verified. On the other hand there may occur isolated populations of non-endemic species at this places too. Although we cannot exclude a secondary immigration (even with human influence, see below) they may support our conclusions.

B. Biogeographic reference for the refugia near Basel and Salzburg

B. 1. The refugia in general

Many of the classical localities of former investigators have been visited and in most cases it was possible to confirm the occurence. It has been proved, that the genera *Haasea*, *Xylophageuma*, *Syngonopodium*, *Pyrgocyphosoma*, *Rhymogona* and *Listrocheiritium* perform the condition of being relatively easy to find. It is most important to choose the right time. At the middle to late October they will be quite common under bark and dead wood. Nevertheless there are differences between the genera: *Rhymogona* and *Pyrgocyphosoma* will be found quite regulary in October, with no or only minute dependence from the weather. In spite of BIGLER's (1913) opinion *P. titianum* is quite common, but strongly related to high humidity, so that it is mostly found near springs and small brooks. *Xylophageuma vomrathi* is much more difficult to catch, possibly contrary to its sibling species *X. zschokkei*, that was found quite common by PEDROLI-CHRISTEN and myself during our excursions in the Vosges Mountains and the Jura. But although we both collected *Pyrgocyphosoma* and *Rhymogona* quite regulary, PEDROLI-CHRISTEN has never found *X. vomrathi*. Its occurence seems to depend on cold weather with temperatures just above the freezing-point.

Other species, like the possibly phreatic ones *Alpityphlus seewaldi* (only one record known, STRASSER, 1967), *Polydesmus rothi* and *P. xanthocrepis* have very seldom been collected and seem to be not suitable for a survey. Nevertheless, as long as we have no contradictions for their endemism, we may use them as additional arguments for the refugia.

At the investigated sites the endemic species have been found sympatric and often syntopic under the same bark, in community with a rich fauna of other millipedes. During the investigations, at two places (Hasel, Scharfling) the maximal amount of endemic Chordeumatida has been found syntopic. This supports the assumption of a glacial refuge and contradicts the conception that the endemism results from competition with superior species.

Both refugia contain limestone areas. This might be of general importance for glacial refugia, as calcareous areas mean warmer soil and the crevices provide places with moderate, although cold climatic conditions, that may render a retreat during hard times.

B. 2. The "Basel-refuge"

When comparing the maps (Figs 1-3) *P. titianum* shows the most closed distribution of its records, so that it is regarded as the most suitable species for reconstructing the "Basel-refugium". The three endemic *Rhymogona*-species indicate a partition to at least three different sites. A possibly similar species-complex occurs in the snail genus *Bythiospeum*.

Another endemic animal in the southern Black Forest is the earthworm *Lumbricus badensis*. Its distribution (KOBEL-LAMPARSKI & LAMPARSKI, 1989) is much the same as in *P. titianum*. Other endemisms in this region are known from snails (*Bythinella badensis*, *Bythiospeum sterkianum*, SCHMID, 1979; SCHMID, 1989). In the snail genus *Trichia* 4 endemic species are known from northern Switzerland and adjacent Germany (*T. caelata*, *T. clandestina*, *T. graminicola*, *T. biconica*, KERNEY *et. al.*, 1983), with *T. caelata* having a similar distribution as *Polydesmus rothi* (Fig. 1). In the caves of the northern Jura the endemic cave-beetle *Royerella villardi matheyi* occurs. Somewhat more southward in the Jura we will find other cave animals like *Trichaphaenops sollaudi* (Coleoptera), *Trichoniscoides pulchellus* (Isopoda),

Source : MNHN, Paris

Archiboreoiulus sollaudi and *Boreoiulus simplex* (both Diplopoda). As a support from wider distributed species we have isolated populations of subalpine plants like *Primula auricula* (MEUSEL *et al.*, 1965-92) and beetles like *Nebria gyllenhali* (missing in the Vosges Mountains) that occur in the Black Forest.

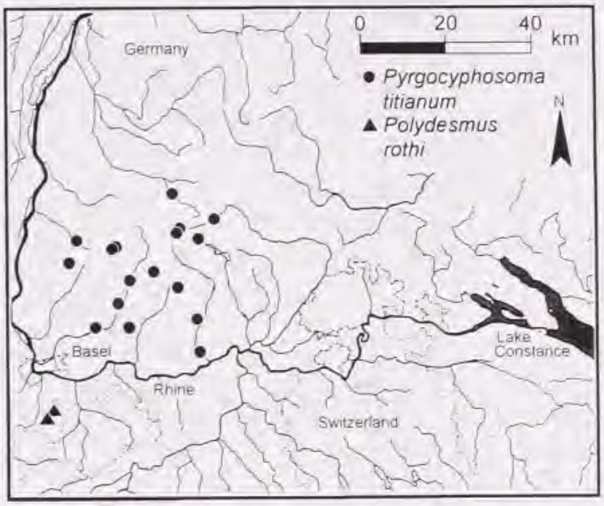


FIG. 1. — Distribution of *Pyrgocyphosoma titianum* and *Polydesmus rothi* in southwestern Germany and adjacent Switzerland.

The lack of the endemic Black-Forest-species, as well as related species in Switzerland (PEDROLI-CHRISTEN, 1993), at the alpine level contradicts a nunatak-refuge and supports a massif de refuge at lower altitudes. When we decrease the formerly glaciated areas (HANTKE, 1978-1983), the calcareous mountains at the southern border of the Black Forest remain as most probable refuge. This might be supported by the sympatric occurence of members of all three endemic genera and the junction of the ranges of the three endemic *Rhymogona*-species. In agreement with a map provided by HANTKE (1978-1983) we are even able to attach the ice-free parts of the southern Black Forest as refugia to each of the endemic *Rhymogona*-species.

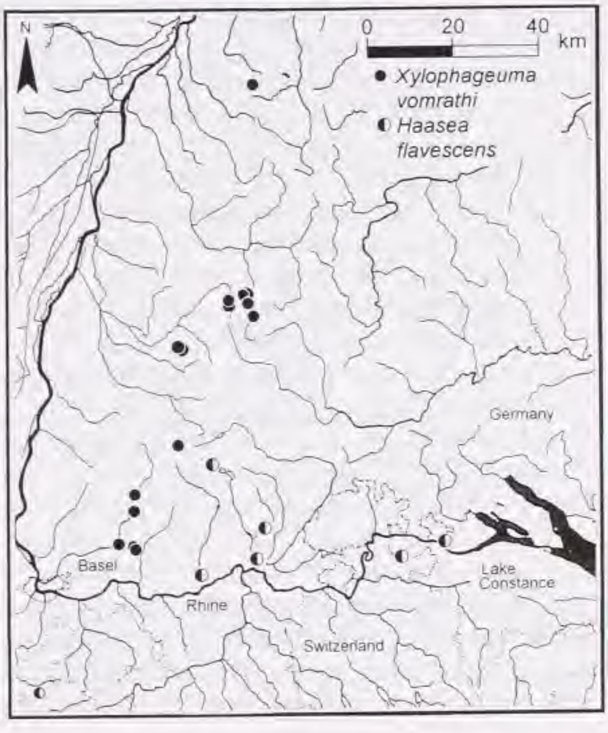


FIG. 2. — Distribution of *Xylophageuma vomrathi* and *Haasea flavescens* in southwestern Germany and adjacent Switzerland.

Source : MNHN, Paris

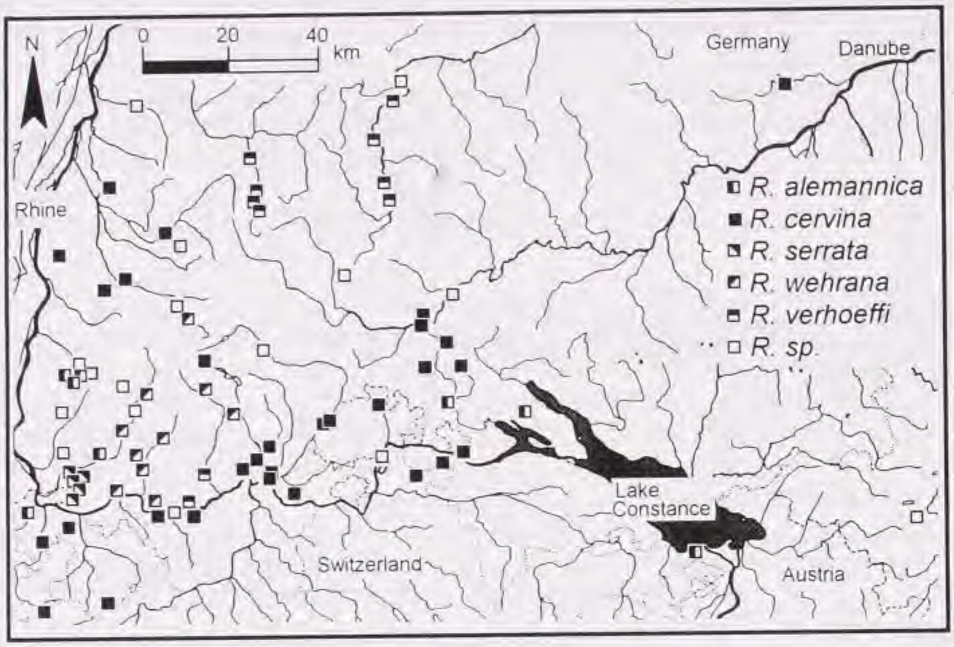


FIG. 3. — Distribution of *Rhymogona* species in southwestern Germany and adjacent Switzerland.

B. 3. The "Salzburg-refuge"

The "Salzburg-refuge" can be delimited by the occurence of *Syngonopodium aceris*, *Haasea norica* and *Listrocheiritium noricum* (Figs 4-6). At present time we still have gaps in the knowledge of the millipede fauna in northern Austria, so that not too many conclusions about the exact extension of the refuge should be drawn. The results are in accordance with HOLDHAUS (1954), and we can add the beetles *Trechus wagneri* and *Otiorhynchus schaubergeri* as further endemisms of this region. Very interesting is the occurence of the also endemic cave beetle *Trichaphaenops angulipennis* in the Dachstein-mountains, an area regarded as beeing glaciated during the Würm. But as phreatic/cave species are difficult to record this species might have survived at the unglaciated sites nearby. Its distribution resembles *Syngonopodium cornutum*. As the eastern Alps have only been slightly glaciated (HOLDHAUS, 1954), the number of endemic species increases eastward, so that we might assume a series of refugia along the northern Alps from Salzburg on. This is supported by the distribution of the genus *Listrocheiritium*, showing a sequence of species there. The isolated record of *L. nubium* in the mountains of the "Totes Gebirge" is very strange and may refer to *L. noricum* as a possible misidentification. *L. cervinum* has a wider distribution inside the Alps, and the new record ("Tauernalm") fills the gap between the mountains of Hochstaufen, Grimming and Großglockner. *Listrocheiritium*-species show a large vertical distribution, reaching the alpine level and have possibly survived on both, nunataks and massifs de refuge. The Austrian record of *L. septentrionale* (Rossatz) is identical with "Buchental bei Spitz" given by ATTEMS (1949) as locality for the never described *L. nibelungiacum*. Examination of topotypic specimen and ATTEMS' types proved their identity, although *L. septentrionale* has been described from a site more than 80 km northerly. This may show, that in contrast to VERHOEFF'S (1917) opinion large rivers like the Danube provide no hindrance for Chordeumatida. As most parts of northern

Source : MNHN, Paris

Austria are myriapodological badly investigated this species might be well distributed in the intermediate area.

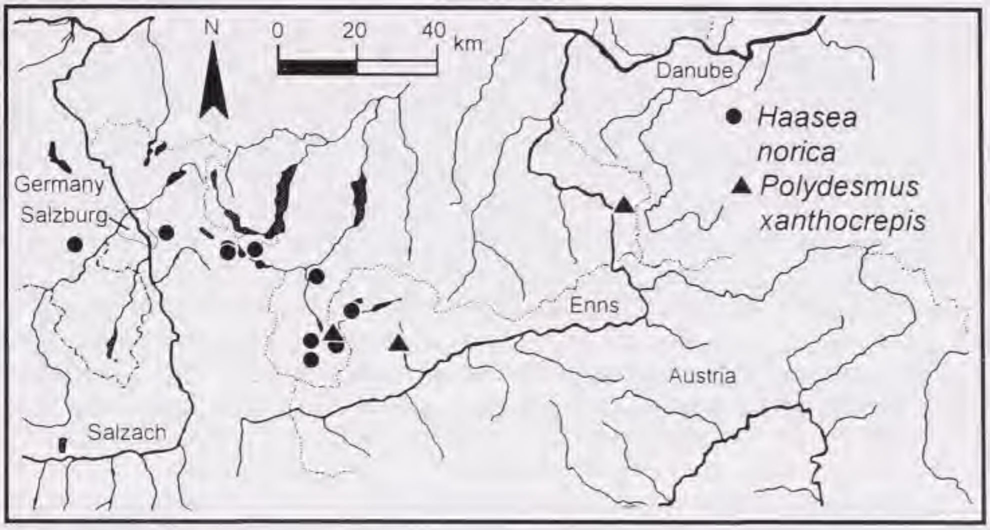


FIG. 4. — Distribution of *Haasea norica* and *Polydesmus xanthocrepis* in the northeastern Alps.

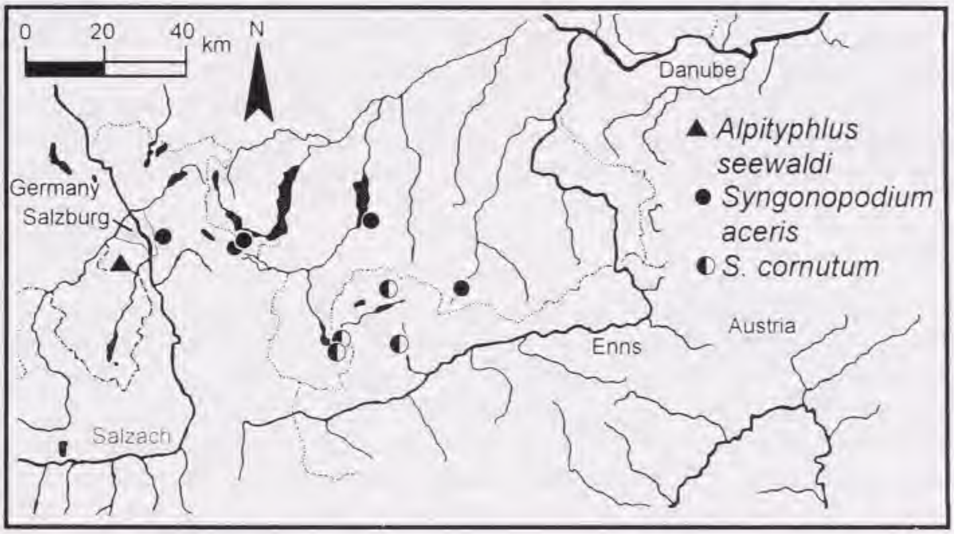


FIG. 5. — Distribution of *Alpityphlus seewaldi* and *Syngonopodium* species in the northeastern Alps.

Isolated populations of wider distributed species, that support the "Salzburg-refuge" are found in many snails e.g. *Acicula gracilis* and *Renea veneta* (KERNEY *et al.*, 1983). In respect of this, the isolated occurence of the chordeumatid *Haplogona oculodistincta* at Scharfling is very interesting, as it could belong to a relict population. As this site provides a rich, pretentious

Source : MNHN, Paris

millipede fauna, synanthropism might be excluded. The species is distributed in the southeastern Alps up to Vienna and adjacent Balkan Peninsula.

C. Discussion of problems and counter-arguments

C. 1. Speciation after the Ice Age

Someone may argue, that the endemic species have been developed after the time of glaciation. An argument for this is the occurrence of endemic plants like the *Papaver radicatum* complex, on which a discussion for ice-free refugia in Scandinavia was based on. NORDAL (1987) showed, that we can explain the endemism by postglacial immigration and subsequent speciation. This is certainly in larger accordance with the geological results there. The question is, can we transfer this to animals? The arguments against are, that we have no similar endemisms of animals in Scandinavia, and that plant "speciation" can occur extremely rapid by a single mutation with distinct phenotypic effect. As the presence of a mate is not absolutely necessary (self fertilisation) a single specimen can be the ancestor of a whole changed population beside a refuge. Animals, if not parthenogenetic, are liable to bisexual propagation, that will suppress extraordinary mutations if they are not advantageous. In times of spreading, when there are less meetings of males and females sexual selection would be less effective (EBERHARD, 1985).

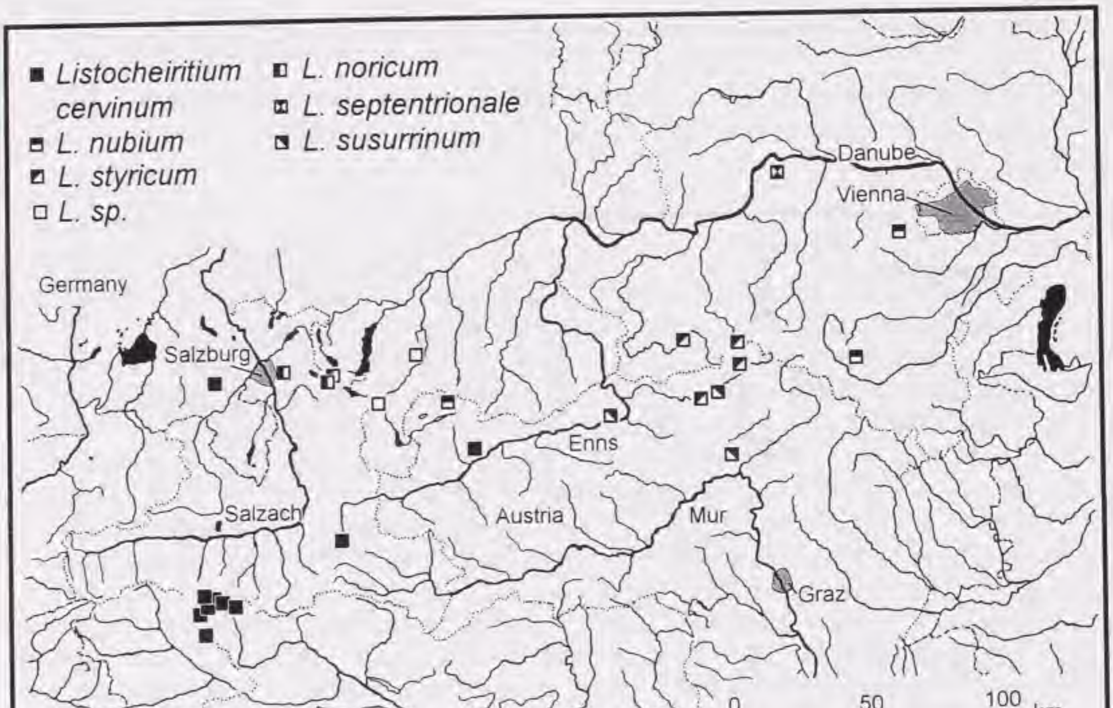


FIG. 6. — Distribution of *Listrocheiritium* species in the northeastern Alps.

C. 2. The character of natural borders

VERHOEFF (1917) was the first who discovered the importance of rivers as distributional borders. An argument against them as absolute borders for millipedes might be the occurence of species with generally small ranges on both sides of the Danube (*Listrocheiritium septentrionale*,

Source : MNHN, Paris

Haploporatia eremita, *Leptoiulus marcomannius*) and the Rhine (*Rhymogona cervina*, *R. alemannica*, *Orthochordeumella fulva*, *Polydesmus helveticus*, "Helvetischer Rheintaldurchbruch" of VERHOEFF, 1917).

With respect to EBERHARD's (1985) hypotheses I will propose another explanation. If two species have been separated only by sexual selection they still use the same ecological niche. As we know that two species cannot occupy the same niche at the same time, they must occur allopatric or parapatric (vicariance). If we assume that their selective fitness is quite equal, the native species is in favour against the invasive. As a result we will have relative stable borders at places that will not be crossed so often like rivers and mountain ridges. This explains the complex distribution of the genus *Rhymogona* in southwestern Germany much better, as the distribution follows small rivers and brooks with species often changing between parallel ones and - on the other hand - changing between larger rivers like the Rhine and the lower course of the Wiese. The parapatric distribution of the related species *Xylophageuma vomrathi* and *Haasea flavescens* (Fig. 2) migth be another case of parapatry by ecological competition.

C. 3. "Natural" extinction

Endemism can not only be explained by speciation e.g. during the ice-age, including reduction of the areal and - up to now - only a minute reimmigration, but also by reduction of the distribution caused by other (ecological) effects like competitors, enemies and diseases. The occurence of such palaeoendemisms may simulate a glacial refuge, but normally in this case we will have more than one isolated population of the same species (meaning places where the hostile conditions are not effective) or they occur on special places, where other species cannot survive (displacement to extreme sites). In spite of this, the places where the endemic millipedes occur contain a very rich fauna so that we may regard displacement as less probable.

C. 4. Human influences

There might be the possibility that a species is delimited to a small area that cannot be left naturally. But if transported by men, perhaps with the earth surrounding a plant, it may arrive a place where spreading means no problem. This has been followed quite profound in North America by the invasion of European species. Perhaps this is also a good explanation for the colonization of the British Island by millipedes, as they might have been companions of early settlers. On the other hand devastation by men took part in many of the areas populated by him, e.g. by cutting down the forest. So we might also think of the change of areals by men in recent and former days.

CONCLUSIONS

Comparison of the refugia presented here with the map of true cave-animals given by HOLDHAUS (1954) shows, that the northernmost parts of their distribution cover with them. Also a map provided by JANETSCHEK (1956) shows our refugia being included, but as demonstrated here, they are more ensured and obviously of larger importance than most of the other north-alpine "refugia" shown by him. So there is much evidence, that the southern part of the Black Forest and the mountains of the Salzkammergut are the northernmost places where a pretentious fauna have survived at least the last glaciation (Würm) in middle Europe (excluding the Carpathians). Although there might have been no larger trees, there is much evidence that *Salix*-species have survived the last cold stage north of the Alps (BENNET *et al*, 1991). Their litter might have served as food for the persistent diplopods.

An interesting aspect has been pointed out on forest trees by BENNET *et al.* (1991), saying that remainig tree populations at mid-altitude sites in the mountainous areas of southern Europe are most important for the long-term survival of species, as they cannot follow the rapid climatic changes. As a result, the refugia are important at all times, both cold and warm stages. This might also be true for animals with a low tendency of spreading out and may explain the "petrophilism" just because of the fact that mountains show closed sites with different climatic

Source : MNHN, Paris

conditions, that allow changes to suitable biotopes, so that a long-distance travelling to such places is not necessary in cases of global climatic changes.

As no one can travel through time and test hypotheses concerning the past, we have to use the "principle of parsimony", that is also used in the discussion of phylogenetic pathways, meaning that we favour hypotheses that need less additional assumptions than others. The present distribution of organisms seems to be an important argument in cases where we have no pollen evidence or macrofossils. With the exception of three phreatic/cave species (*Alpityphlus seewaldi*, *Polydesmus xanthocrepis* and *P. rothi*) the endemic millipedes all belong to the Chordeumatida. This shows, that the members of this order are the most important indicators for our purpose.

Up to now, no other group is known, showing so much endemism in the European mountains as the millipedes (VERHOEFF, 1938b) and especially the chordeumatids. These species - "Glazialresistente" of VERHOEFF (1917) - must be considered as beeing preglacial or at least interglacial relicts.

ACKNOWLEDGMENTS

The author is greatly indebted to Professor Dr. h. c. Burkhard FRENZEL (University of Stuttgart-Hohenheim, Institut of Botany), Dr. Sergei I. GOLOVATCH (Russian Academy of Science, Moscow) and Prof. Dr. Hinrich RAHMANN (University of Stuttgart-Hohenheim, Institut of Zoology) for giving valuable advices. I also wish to thank my colleagues Dr. Jürgen BÖHMER and Dietmar ROTHMUND for critical reading of the manuscript.

REFERENCES

ATTEMS, C., 1949. — Die Myriopodenfauna der Ostalpen. *SB Ak. Wien., math.-naturw. Kl, I*, **158** : 79-153.

BENNETT, K. D., TZEDAKIS, P. C. & WILLIS, K. J., 1991. — Quaternary refugia of north European trees. *J. Biogeogr.*, **18** : 103-115.

BIGLER, W., 1913. — Die Diplopoden von Basel und Umgebung. *Rev. suisse Zool.*, **21** : 675-793.

EBERHARD, W. G., 1985. — *Sexual selection and animal genitalia*. Cambridge & London, C.U.P., 255 pp.

HANTKE, R., 1978. — *Eiszeitalter*. Thun, Vol. 1, 467 pp.

HANTKE, R., 1980. — *Eiszeitalter*. Thun, Vol. 2, 703 pp.

HANTKE, R., 1983. — *Eiszeitalter*. Thun, Vol. 3, 730 pp.

HOLDHAUS, K., 1954. — Die Spuren der Eiszeit in der Tierwelt Europas. *Abh. zool.-bot. Ges. Wien*, **18** : 1-493.

JANETSCHEK, H., 1956. — Das Problem der inneralpinen Eiszeitüberdauerung durch Tiere (Ein Beitrag zur Geschichte der Nivalfauna). *Österr. zool. Zeitschrift*, **6** : 421-506.

KERNEY, M. P., CAMERON, R. A. D. & JUNGBLUTH, J. H., 1983. — *Die Landschnecken Nord- und Mitteleuropas*. Hamburg & Berlin, Paul Parey, 384 pp.

KOBEL-LAMPARSKI, A. & LAMPARSKI, F., 1989. — Der Badische Regenwurm *Lumbricus badensis* und andere bemerkenswerte Regenwürmer aus dem Belchengebiet. *In : Der Belchen. Natur- und Landschaftschutzgebiete Bad.-, Württ.*, Karlsruhe, **13** : 891-905.

MEUSEL., H., JÄGER, E. J. & WEINERT, E., 1965. — *Vergleichende Chorologie der zentraleuropäischen Flora. Vol. 1*, Jena, 582+258 pp.

MEUSEL., H., JÄGER, E. J. & WEINERT, E., 1978. — *Vergleichende Chorologie der zentraleuropäischen Flora. Vol. 2*, Jena, 418+162 pp.

MEUSEL., H., JÄGER, E. J. & WEINERT, E., 1992. — *Vergleichende Chorologie der zentraleuropäischen Flora. Vol. 3*, Jena, 333+256 pp.

NORDAL, I., 1987. — Tabula rasa after all? Botanical evidence for ice-free refugia in Scandinavia reviewed. *J. Biogeogr.*, **14** : 377-388.

PEDROLI-CHRISTEN, A., 1993. — Faunistique des mille-pattes de Suisse (Diplopoda) / Faunistik der Tausendfüssler der Schweiz (Diplopoda). Neuchâtel, Centre Suisse de Cartographie de la Faune, *Doc. faun. helv.*, **14**, 248 pp.

SCHMID, G., 1979. — Mollusken vom Grenzacher Horn. *In : Der Buchswald bei Grenzach (Grenzacher Horn). Natur- und Landschaftschutzgebiete Bad.-Württ.*, Karlsruhe, **9** : 225-359.

SCHMID, G., 1989. — Schnecken und Muscheln vom Belchen. *In : Der Belchen. Natur- und Landschaftschutzgebiete Bad.-Württ.*, Karlsruhe, **13** : 891-905.

Source : MNHN, Paris

SPELDA, J., 1991. — Zur Faunistik und Systematik der Tausendfüßler (Myriapoda) Südwestdeutschlands. *Jh. Ges. Naturkde. Württemberg*, **146** : 211-232.

STRASSER, K., 1967. — Ein Typhloiuline aus den nördlichen Kalkalpen (Diplopoda, Symphyognatha). *Ber. nat.-med. Ver. Innsbruck*, **55** : 145-154.

VERHOEFF, K. W., 1917. — Zur Kenntnis der Zoogeographie Deutschlands zugleich über Diplopoden namentlich Mitteldeutschlands und Beiträge für die biologische Beurteilung der Eiszeiten. *Nova Acta. Abh. der Kaiserl. Leop.-Carol. Deutschen Akademie der Naturforscher*, **103** : 1-157.

VERHOEFF, K. W., 1938a. — Diplopoden der Germania zoogeographica im Lichte der Eiszeit. *Zoogeographica*, **3** : 494-547.

VERHOEFF, K. W., 1938b. — Ein halbes Jahrhundert Diplopodenforschung und ihre Bedeutung für die Zoogeographie. *Zoogeographica*, **3** : 548-588.

Source : MNHN, Paris

Source : MNHN, Paris

On the Distribution and Faunogenesis of Himalayan Millipedes (Diplopoda): Preliminary Results[1]

Sergei I. GOLOVATCH * & *Jochen MARTENS* **

* Institute for Problems of Ecology and Evolution, Russian Academy of Sciences
Leninsky prospekt 33, Moscow V-71, Russia
** Institut für Zoologie, Johannes Gutenberg-Universität
Saarstrasse 21, D-55099 Mainz, Germany

ABSTRACT

The fauna of Diplopoda of the Himalayas (over 200 species, mostly endemic) is reviewed, with particular reference to that of their central part. In spite of the preliminary state of knowledge, the patterns of vertical and geographic distributions suggest the fauna to be eventually entirely Oriental and/or Indian in origin, and primarily associated with forest tropical and/or subtropical communities. The so-called Palearctic influence in the relatively well-explored Central Himalayas actually also originates in the present-day subtropical regions of Southeast and East Asia. The Himalayas seem to have served as a pathway for repeated spreads of a uniform Turgai biota (with Diplopoda being an accompanying group) which, chiefly during the early and middle Tertiary, advanced northwestward, following the receding southern coast of the Tethys Sea. Naturally, during their relatively short orogenic history, the Himalayas also served as a major center of secondary diversification for numerous groups, especially during the Plio-Pleistocene.

RÉSUMÉ

Répartition et genèse des faunes de Diplopodes de l'Himalaya : résultats préliminaires.

La faune des diplopodes des massifs himalayens (plus de 200 espèces, la plupart endémiques), plus particulièrement de leur partie centrale, est révisée. Les modalités de la répartition verticale et géographique suggèrent pour cette faune une origine entièrement orientale et/ou indienne, primitivement associée à des peuplement forestiers tropicaux et/ou subtropicaux. L'influence dite paléarctique provient, dans les régions relativement bien explorées des chaînes centrales de l'Himalaya, des aires subtropicales actuelles du Sud-Est et de l'Est asiatique. Les massifs himalayens semblent avoir servi de "bordure" à des extensions répétées d'un type d'écosystème uniforme de type "Turgai" (les diplopodes apparaissant comme un groupe accompagnateur) qui, surtout durant le début et le milieu de l'ère tertiaire, a progressé vers le Nord-Ouest à la suite du recul de la côte méridionale de la Téthys. Bien entendu, durant cette histoire orogénique relativement courte, les massifs himalayens ont été également un centre majeur de diversification secondaire pour de nombreux groupes d'êtres vivants, notamment au cours du Plio-Pléistocène.

---

1 Results of the Himalaya Expeditions of J. Martens, No. 201. — For No. 200 see: Bonner Zoologische Monographien, 39, 1995. — J. M. sponsored by Deutscher Akademischen Austauschdienst, Deutsche Forschungsgemeinschaft and Feldbausch Foundation, Fachbereich Biologie, Universität Mainz.

GOLOVATCH, S. I. & MARTENS, J., 1996. — On the distribution and faunogenesis of Himalayan millipedes (Diplopoda): preliminary results. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 163-174. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

INTRODUCTION

Being one of the globe's greatest mountainous lands supporting the highest peaks such as Everest, Kanchenjunga, Manaslu, Annapurna, etc., the Himalayas occupy a vast area encompassing the ranges lying between the rivers Indus and Brahmaputra and roughly delimited by 74°E in the west and 95°E in the east (Fig. 1). The adjacent Karakorum and Kohistan-Baluchistan regions in the west, and the Arakan-Chin-Yoma fold belt and the Magok belt in the east are of the same orogenesis (MASCLE *et al.*, 1990).

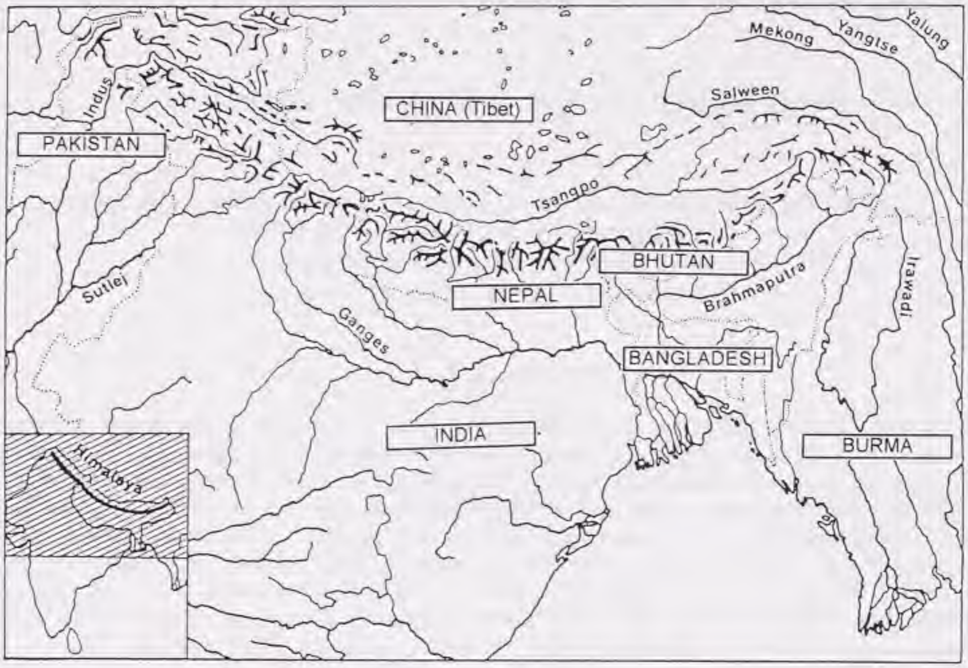


FIG. 1. — Orography of the Himalayas.

From a biologist's viewpoint, the Himalayas represent a highly important barrier between the cold and arid uplands of Central Asia and largely tropical South and Southeast Asia, reinforcing the contrast and, in spite of numerous local inversions, creating their own climate. During the southwestern monsoon period, precipitation mainly occurs on the southern slopes, being greatly reduced on the northern ones. However, this barrier function holds true only for the central parts of the mountains, more or less within Kumaon, Nepal, Sikkim, and Bhutan. In the western Himalayas, the aridity of Central Asia extends across the southern slopes, while in the eastern parts rainstorms, though declining in amount and frequency, reach as far as Southeast Tibet (TROLL, 1967).

This drastic climatic gradient within the Central Himalayas is of great importance, influencing the distribution of various organisms. Although phyto- and zoogeographic regions differ in certain details, both emphasize the role of the Himalayas as a contact region between two great biogeographic realms, the Palearctic and Oriental, which meet and intermesh there in various ways. All areas north of the Central Himalayas obviously belong to the Palearctic, as do the highest parts of the inhabited southern flanks. The lower and lowest altitudes of the southern slopes are largely attributable to the Oriental realm. However, the border between both regions is generally neither striking nor abrupt, forming more (especially in the eastern Himalayas) or less (in their central parts) vast transition areas, numerous inversions or anomalies. In other words, the otherwise manifest rule "(sub)tropical organisms for (sub)tropical environments only" is

Source : MNHN, Paris

very often violated in the Himalayas, particularly in the central parts of this great mountainous land and especially as regards animals (e.g. MARTENS, 1984, 1993). Even the altitudinal zonation of Himalayan plant communities is rather conventional (DOBREMEZ, 1972) (Fig. 2).

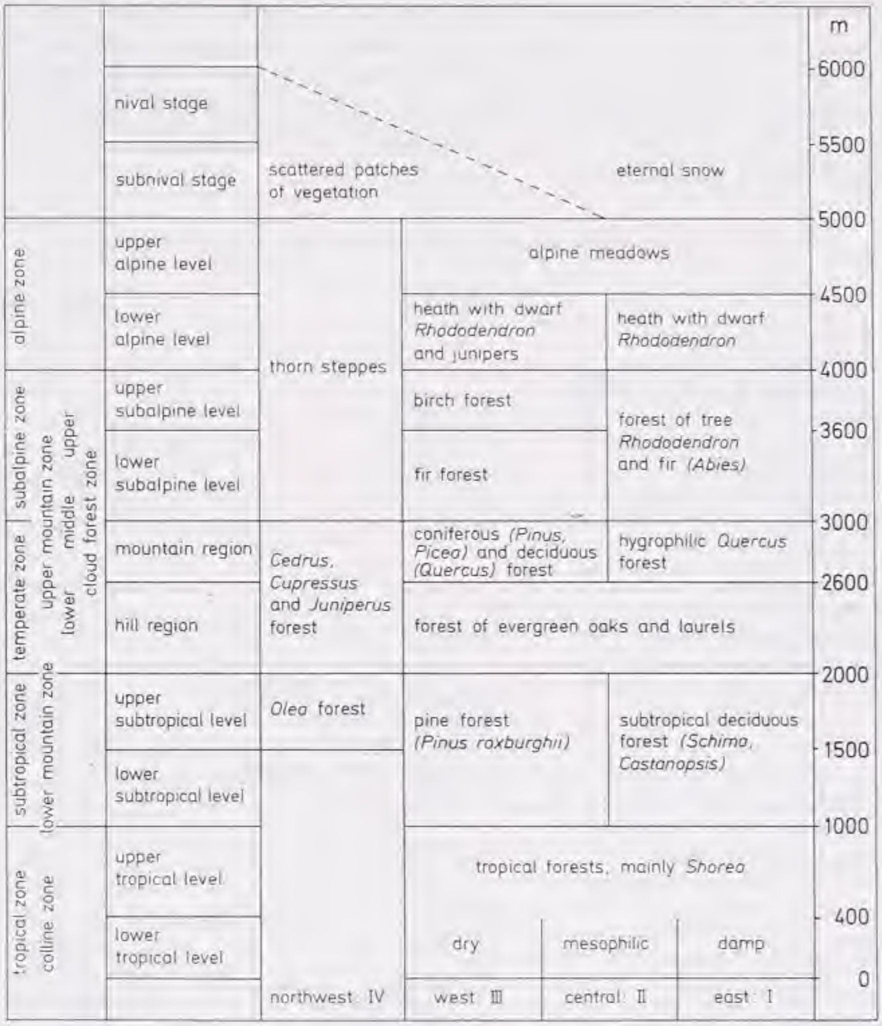


FIG. 2. — The vegetation belts and most important plant communities in the Nepal Himalayas. The Roman numerals at the bottom indicate the floral regions of Nepal (modified, after DOBREMEZ, 1972).

The present paper is the first attempt to trace the vertical distribution patterns of Himalayan millipedes which is basic for reliable faunogenetic reconstructions. This study is mainly restricted to the fauna of Nepal, the Himalayas' centralmost and particularly well-explored part, but all available information is also incorporated on the faunas of adjacent areas and of some ecologically similar soil/litter-dwelling animal groups for comparative purposes. At the start, these results must be regarded as quite preliminary, for a considerable proportion (perhaps over 50%) of the existing collections of Diplopoda remains untreated. In addition to published material, certain unpublished data are presented, chiefly derived by the senior author from the long-term research project conducted by the junior author and his collaborators since 1969 (MARTENS, 1987a; GOLOVATCH, 1990). In spite of its preliminary character, this paper seems warranted to draw some general conclusions on the patterns of diplopod faunogenesis. The latter

Source : MNHN, Paris

is the main objective, while the patterns of altitudinal distribution of Himalayan millipedes are an important tool.

DIPLOPODA OF THE HIMALAYAS

Table 1 presents all available information on the millipede fauna of, and its distribution within, the Himalayas, with over 200 species represented. However, some taxonomic remarks are necessary. A few genera are between quotation marks, for they are obscure either as taxa or as Himalayan elements (see HOFFMAN, 1980). In some cases, no information on elevations is available, this being reflected by a question mark [(?)]. Introductions (N° 183-184) are extremely rare and are referred to as synanthropic.

TABLE 1. — Geographic and vertical distribution of Himalayan diplopods.

TAXA	COUNTRY	ELEVATIONS (m.)
Order Polyxenida		
Family Polyxenidae		
Genus *Polyxenus* Latreille, 1802-03		
1. *Polyxenus* sp.	Kashmir	1585
Genus *Monographis* Attems, 1907		
2. *M. mirus* (Turk, 1947)	Kumaon	1600
Genus *Unixenus* Jones, 1944		
3. *Unixenus* sp.	Nepal	4550
Order Sphaerotheriida		
Family Sphaeropoeidae		
Genus *Indosphaera* Attems, 1936		
4. *Indosphaera curiosa* Attems, 1936	Assam	?
Genus *Kophosphaera* Attems, 1936		
5. *K. brevilamina* Attems, 1936	North Bengal, Darjeeling Distr.	1700
6. *K. devolvens* Attems, 1936	Sikkim, Darjeeling Distr.	1700-2050
7. *K. excavata* (Butler, 1874)	Nepal, Assam	?
8. *K. excavata mammifera* Attems, 1936	Darjeeling Distr., Assam	?
9. *K. politissima* Attems, 1936	Darjeeling Distr.	1700
Genus *"Sphaeropoeus"* Brandt, 1833		
10. *S. montanus* Karsch, 1881	Himalayas	?
Genus *"Sphaerotherium"* Brandt, 1833		
11. *S. maculatum* Butler, 1874	Sikkim	?
12. *S. politum* Butler, 1874	Sikkim	?
Genus *"Zephronia"* Gray, 1832		
13. *Z. alticola* Attems, 1936	Assam, Darjeeling Distr.	400-1700
14. *Z. debilis* Attems, 1936	Darjeeling Distr.	1700
15. *Z. densipora* Attems, 1936	Assam	?
16. *Z. disparipora* Attems, 1936	Assam	140
17. *Z. hirta* Attems, 1936	Darjeeling Distr.	1700
18. *Z. hysophila* Attems, 1936	Assam	?
19. *Z. juvenis* Attems, 1936	Assam	?
20. *Z. laevissima* Butler, 1874	Sikkim	?
21. *Z. lignivora* Attems, 1936	Assam	180-330
22. *Z. manca* Attems, 1936	Vietnam, Darjeeling Distr.	1000-1700
23. *Z. nigrinota* Butler, 1872	Darjeeling Distr.	2300-2700
24. *Z. specularis* Attems, 1936	Assam	?
25. *Z. tigrinoides* Attems, 1936	Darjeeling Distr.	170
26. *Z. tumida* Butler, 1882	Assam, Burma	?
27. *"Zephronia"* spp.	Nepal	250-500
Order Glomerida		
Family Glomeridae		
Genus *Hyleoglomeris* Verhoeff, 1910		
28. *H. crassipes* Golovatch, 1987	Nepal	2450-2720
29. *H. electa* Silvestri, 1917	Darjeeling Distr.	500-1700

Source : MNHN, Paris

30. *H. gorkhalis* Golovatch, 1987	Nepal	1200
31. *H. khumbua* Golovatch, 1987	Nepal	3250-3300
32. *H. modesta* Silvestri, 1917	Assam	150
33. *H. nagarjunga* Golovatch, 1987	Nepal	1900-2100
34. *H. tinjurana* Golovatch, 1987	Nepal	2450
35. *H. venustula* Silvestri, 1917	Assam	?
Order Siphonophorida		
Family Siphonophoridae		
Genus *Pterozonium* Attems, 1951		
36. *P. cingulatum* (Attems, 1936)	Vietnam, Darjeeling Distr.	500-1700
37. *P. coniceps* (Attems, 1936)	Darjeeling Distr.	1700
38. *P. larwoodi* (Turk, 1947)	Kumaon	1600
Order Platydesmida		
Family Andrognathidae		
Genus *Pseudodesmus* Pocock, 1887		
39. *?Pseudodesmus* sp.	Nepal	<2000
Order Chordeumatida		
Family Cleidogonidae		
Genus *Tianella* Attems, 1904		
40. *T. ausobskyi* Shear, 1987	Nepal	2500-3050
41. *T. bobanga* Shear, 1979	Nepal	2460-2500
42. *T. daamsae* Shear, 1987	Nepal	3600-3900
43. *T. gitanga* Shear, 1987	Nepal	2550
44. *T. jaljalensis* Mauriès, 1988	Nepal	2350
45. *T. kathmandua* Mauriès, 1988	Nepal	1700
46. *T. lughla* Shear, 1979	Nepal	2950-3300
47. *T. mananga* Shear, 1987	Nepal	2550
48. *T. mangsingma* Mauriès, 1988	Nepal	2250
49. *T. martensi* Shear, 1979	Nepal	1150-2900
50. *T. smetanai* Mauriès, 1988	Nepal	3250
51. *Tianella* sp.	Darjeeling Distr.	900-1400
Family Kashmireumatidae		
Genus *Kashmireuma* Mauriès, 1982		
52. *K. nepalensis* Mauriès, 1988	Nepal	3600-4100
53. *K. nielseni* Mauriès, 1982	Kashmir	2600-3500
54. *K. schawalleri* Shear, 1987	Nepal	3450-3600
55. *Kashmireuma* sp.	Nepal	2500-3000
Family Megalotylidae		
Genus *Nepalella* Shear, 1979		
56. *N. deharvengi* Mauriès, 1988	Nepal	2900-3500
57. *N. gairiensis* Mauriès, 1988	Nepal	3000
58. *N. gunsa* Shear, 1987	Nepal	3600-3800
59. *N. jaljalae* Mauriès, 1988	Nepal	2200
60. *N. khumbua* Shear, 1979	Nepal	3250-3300
61. *N. phulcokia* Mauriès, 1988	Nepal	2250
62. *N. ringmoensis* Mauriès, 1988	Nepal	2750-3000
63. *N. taplejunga* Shear, 1987	Nepal	3000-3300
64. *N. thodunga* Shear, 1979	Nepal	3200
65. *N. tragsindola* Mauriès, 1988	Nepal	2450-3000
66. *Nepalella* sp.	Nepal	1900-4100
Order Julida		
Family Julidae		
Genus *Anaulaciulus* Pocock, 1895 (cf. KORSÓS, 1996)		
67. *A. acaudatus* Korsós, 1996	Sikkim	3990
68. *A. bilineatus* Korsós, 1996	Nepal	3300-4300
69. *A. kashmirensis* Korsós, 1996	Kashmir	3100-3200
70. *A. nepalensis* Korsós, 1996	Nepal	2600-3400
71. *A. niger* Korsós, 1996	Nepal	2600-4500
72. *A. tibetanus* Korsós, 1996	China (E-Tibet), Assam	3700
73. *A. topali* Korsós, 1996	Kashmir	2300

Source : MNHN, Paris

Genus *Nepalmatoiulus* Mauriès, 1983		
74. *N. appendiculatus* Enghoff, 1987	Kumaon	1900-2100
75. *N. deharvengi* (Mauriès, 1983)	Nepal	2550-3350
76. *N. dhaulagiri* Enghoff, 1987	Nepal	3000-3350
77. *N. generalis* Enghoff, 1987	Nepal	3400
78. *N. hyalilobus* Enghoff, 1987	Nepal	3600-3800
79. *N. ivanloebli* Enghoff, 1987	Nepal	2200-4800
80. *N. juxtapositus* Enghoff, 1987	Nepal	2800-3050
81. *N. martensi* Enghoff, 1987	Nepal	3250-3300
82. *N. mauriesi* Enghoff, 1987	Nepal	3600
83. *N. nigrescens* Enghoff, 1987	Bhutan	2300
84. *N. pineti* Enghoff, 1987	Nepal	2900
85. *N. rugiflagrum* Enghoff, 1987	Bhutan	3300
86. *N. smetanai* (Mauriès, 1983)	Nepal	1900-2700
87. *N. sympatricus* Enghoff, 1987	Nepal	3000
88. *N. uncus* Enghoff, 1987	Nepal	2550
89. *N. wuermlii* Enghoff, 1987	Bhutan	1680-2600
90. *N. zachonoides* Enghoff, 1987	Nepal	2450-2600
Order Spirostreptida		
Family Harpagophoridae		
Genus *Gonoplectus* Chamberlin, 1921		
91. *G. alius* Demange, 1961	Assam	?
92. *G. bhutanensis* Demange, 1988	Bhutan	350-450
93. *G. broelemanni* Demange, 1961	Nepal	1800-2300
94. *G. corniger* (Attems, 1936)	Assam	?
95. *G. gracilis* (Attems, 1936)	Darjeeling Distr.	1200
96. *G. hyatti* Demange, 1961	Nepal	1200
97. *G. lindbergi* Demange, 1961	Darjeeling Distr., Bhutan	350
98. *G. malayus* (Carl, 1909)	Kumaon, Nepal, Bhutan	200-2500
99. *G. probus* (Attems, 1936)	Darjeeling Distr.	1000
100. *G. remyi* Demange, 1961	Assam	?
101. *G. sulcatus* (Attems, 1936)	Darjeeling Distr.	2400
Order Cambalida		
Family Cambalopsidae		
Genus *Podoglyphiulus* Attems, 1909		
102. *P. elegans nepalensis* Mauriès, 1983	Nepal	<1000
Genus *Trachyjulus* Peters, 1864		
103. *T. mimus* Silvestri, 1924	Assam	1200
104. *T. wilsonae* Mauriès, 1983	Nepal	<1000
Order Spirobolida		
Family Physobolidae		
Genus *Physobolus* Attems, 1936		
105. *P. olivaceus* Attems, 1936	Darjeeling Distr.	1800.
Order Polydesmida		
Family Cryptodesmidae		
Genus *Trichopeltis* Pocock, 1894		
106. *T. watsoni* Pocock, 1894	Darjeeling Distr., Assam, Bhutan, West Bengal, Bangladesh	350-1000
Family Fuhrmannodesmidae		
Genus *Assamodesmus* Manfredi, 1954		
107. *A. lindbergi* Manfredi, 1954	Assam	?
Genus *Hingstonia* Carl, 1935		
108. *H. beatae* Golovatch, 1990	Nepal	2400-3500
109. *H. dorjulana* Golovatch, 1988	Bhutan	2450-3100
110. *H. eremita* Carl, 1935	Nepal	2000
111. *H. falcata* Golovatch, 1986	Nepal	2650
112. *H. fittkaui* Golovatch, 1990	Nepal	3550-3650
113. *H. gogonana* Golovatch, 1988	Bhutan	3650-4000
114. *H. pahakholana* Golovatch, 1990	Nepal	2600-2800
115. *H. pelelana* Golovatch, 1988	Bhutan	3300-3400
116. *H. perarmata* Golovatch, 1986	Nepal	3150

Source : MNHN, Paris

117. *H. serrata* Golovatch, 1987	Nepal	3400-3600
118. *H. sympatrica* Golovatch, 1990	Nepal	3550-3650
119. *H. variata* Golovatch, 1987	Nepal	2600-4500
120. *Hingstonia* sp.	Nepal	2200-3900
Genus *Magidesmus* Golovatch, 1988		
121. *M. affinis* Golovatch, 1988	Bhutan	3300-3400
122. *M. bhutanensis* Golovatch, 1988	Bhutan	3100
Genus *Sholaphilus* Carl, 1932		
123. *S. asceticus* Golovatch, 1986	Nepal	1300-1650
124. *S. dalai* Golovatch, 1986	Nepal	2400
125. *S. gompa* Golovatch, 1990	Nepal	2000-2100
126. *S. lama* Golovatch, 1986	Nepal	1800-2000
127. *S. martensi* Golovatch, 1986	Nepal	1100-1850
128. *S. monachus* Golovatch, 1990	Nepal	2050-2150
Genus "*Pseudosphaeroparia*" Carl, 1932		
129. *P. cavernicola* Turk, 1945	Kumaon	2800
Genus *Topalodesmus* Golovatch, 1988		
130. *T. communis* Golovatch, 1988	Darjeeling Distr.	2000-2200
Family Polydesmidae		
Genus *Bhutanodesmus* Golovatch, 1988		
131. *B. velatus* Golovatch, 1988	Bhutan	350-450
Genus *Glenniea* Turk, 1945		
132. *G. bhotiaensis* Golovatch, 1988	Bhutan	350-450
133. *G. indica* Turk, 1945	Kumaon	2800
134. *G. minuscula* Golovatch, 1988	Bhutan	1900-2300
135. *G. perarmata* Golovatch, 1988	Bhutan	1680
136. *G. martensi* (Golovatch, 1987)	Nepal	1200
Genus *Himalodesmus* Golovatch, 1986		
137. *H. audax* Golovatch, 1986	Nepal	2650
138. *H. benefactor* Golovatch, 1987	Nepal	2600-3400
139. *H. faustus* Golovatch, 1987	Nepal	1000-1750
140. *H. parvus* Golovatch, 1987	Nepal	2200
141. *H. prosperus* Golovatch, 1990	Nepal	2600-2800
142. *H. pulcher* Golovatch, 1987	Nepal	2450
143. *H. pygmaeus* Golovatch, 1986	Nepal	3300-3400
144. *H. vigens* Golovatch, 1987	Nepal	2150-2250
Genus *Typhlopygmaeosoma* Turk, 1972		
145. *T. hazeltonae* Turk, 1972	Kumaon	1850
Genus *Usbekodesmus* Lohmander, 1932		
147. *U. buddhis* Golovatch, 1986	Nepal	3300-3400
148. *U. occultus* Golovatch, 1986	Nepal	2300-2800
149. *U. sacer* Golovatch, 1987	Nepal	3300-3400
150. *U. theocraticus* Golovatch, 1990	Nepal	2600-2800
151. *U. theosophicus* Golovatch, 1986	Nepal	3200
152. *Usbekodesmus* sp.	Nepal, Bhutan	3450-4250
Family Opisotretidae		
Genus *Martensodesmus* Golovatch, 1987		
153. *M. bicuspidatus* Golovatch, 1988	Bhutan	1650-2000
154. *M. excornis* Golovatch, 1988	Bhutan	2440
155. *M. himalayensis* Golovatch, 1987	Nepal	1100-1300
156. *M. nagarjungicus* Golovatch, 1987	Nepal	1900-2100
157. *M. sherpa* Golovatch, 1987	Nepal	1200
158. *Martensodesmus* sp.	Nepal, Bhutan	1300-2150
Family Paradoxosomatidae		
Genus *Armolites* Golovatch, 1984		
159. *A. chulingensis* Golovatch, 1994	Nepal	3000-3700
160. *A. communicans* Golovatch, 1992	Nepal	2650
161. *A. similis* Golovatch, 1992	Nepal	2300-2700
162. *A. spiniger* (Attems, 1936)	Darjeeling Distr.	1000-2200
Genus *Hirtodrepanum* Golovatch, 1994		
163. *H. latigonopum* Golovatch, 1994		

Source : MNHN, Paris

Genus *Kaschmiriosoma* Schubart, 1935		
164. *K. contortipes* Schubart, 1935	Kashmir, N-Pakistan	2300-3300
165. *K. nulla* (Attems, 1936)	Himachal Pradesh	1000
166. *K. pleuroptera* (Attems, 1936)	Punjab (Pakistan)	2800
Genus *Kronopolites* Attems, 1914		
167. *K. occidentalis* Golovatch, 1983	Kashmir	1500
Genus *Martensosoma* Golovatch, 1992		
168. *M. elegans* Golovatch, 1992	Nepal	1350
169. *M. foveatum* Golovatch, 1992	Nepal	1800-2000
170. *M. schawalleri* Golovatch, 1992	Nepal	1000-2150
171. *M. silvestre* Golovatch, 1994	Nepal	2000-2600
172. *M. splendens* Golovatch, 1992	Nepal	1650-2150
173. *M. unicolor* (Attems, 1936)	Assam, Darjeeling Distr.	1200-1700
Genus *Nepalomorpha* Golovatch, 1993		
174. *N. arunensis* Golovatch, 1994	Nepal	1850-2150
175. *N. hirsuta* Golovatch, 1994	Nepal	3900-4100
176. *N. kuznetsovi* Golovatch, 1994	Nepal	3000
177. *N. spinigera* (Golovatch, 1992)	Nepal	600-1400
Genus *Orophosoma* Jeekel, 1980		
178. *O. fechteri* Golovatch, 1990	Nepal	2330-3150
179. *O. hingstoni* (Carl, 1935)	Tibet	3400
180. *O. simulans* (Carl, 1935)	Nepal, Tibet	3700
181. *Orophosoma* sp.	Nepal	1750-3450
Genus *Orthomorpha* Bollman, 1893		
182. *"O." almorensis* Turk, 1947	Kumaon	1600
183. *O. coarctata* (Saussure, 1860)	Nepal (synanthr.)	600-650
Genus *Oxidus* Cook, 1911		
184. *O. gracilis* (C. L. Koch, 1847)	Nepal (synanthr.)	570-1200
Genus *Paranedyopus* Carl, 1932		
185. *P. affinis* Golovatch, 1990	Nepal	2475-2700
186. *P. cylindricus* (Carl, 1935)	Nepal, Darjeeling Distr.	1650-2850
187. *P. elongissimus* Golovatch, 1984	Darjeeling Distr.	1000
188. *P. martensi* Golovatch, 1990	Nepal	2250-3600
189. *P. schawalleri* Golovatch, 1990	Nepal	2050-2150
190. *P. similis* Golovatch, 1990	Nepal	2300-3000
191. *Paranedyopus* sp.	Nepal	2450-2900
Genus *Parorthomorpha* Golovatch, 1994		
192. *P. affinis* Golovatch, 1994	Nepal	1400
193. *P. granulosa* Golovatch, 1994	Nepal	2000
194. *P. intermedia* Golovatch, 1994	Nepal	1000-1100
195. *P. longiseta* Golovatch, 1994	Nepal	1400-1600
196. *P. nyakensis* (Golovatch, 1992)	Nepal	2270-2450
197. *P. philosophica* Golovatch, 1994	Nepal	1650-2450
198. *P. spectabilis* Golovatch, 1994	Nepal	2650
199. *P. tergalis* Golovatch, 1994	Nepal	2650
200. *P. tuberculata* Golovatch, 1994	Nepal	3000-3300
Genus *Substrongylosoma* Golovatch, 1984		
201. *S. distinctum* Golovatch, 1984	Darjeeling Distr.	1200-1500
202. *S. falcatum* Golovatch, 1984	Darjeeling Distr.	1400
203. *S. montigena* (Carl, 1935)	Darjeeling Distr.	1200-2300
204. *S. schawalleri* Golovatch, 1993	Nepal	1620-2000
Genus *Topalosoma* Golovatch, 1984		
205. *T. setiferum* Golovatch, 1984	Darjeeling Distr.	900
Genus *Touranella* Attems, 1937		
206. *T. himalayaensis* Golovatch, 1994	Nepal	2300-2700
Family Pyrgodesmidae		
207. Several genera and species	Nepal	450-1200

Source : MNHN, Paris

ZOOGEOGRAPHIC PATTERNS

The vast majority of Himalayan millipede species are local in distribution; there are few relatively widespread species like *Trichopeltis watsoni*. Indeed, most Himalayan millipede species are known from a single locality only, and many others appear to be restricted not only in area, but also in altitude.

Conversely, most genera occur through a range of altitudes, as shown in Figure 3, but are more or less restricted to forests, demonstrating sylvicoly. Table 1 and Figures 2-3 show that the alpine zone of the Central Himalayas is only marginally populated by millipedes, whereas the tropical and subtropical forest belts support the bulk of the fauna. This pattern conforms to general knowledge that millipedes are primarily a class of forest floor-dwellers, which in temperate regions of Eurasis seems trophecologically and historically associated with nemoral (= broadleaved) forest communities (GOLOVATCH, 1987, 1991a). In turn, this pattern provides the basis for faunogenetic reconstructions based on phyto- and paleogeographic evidence.

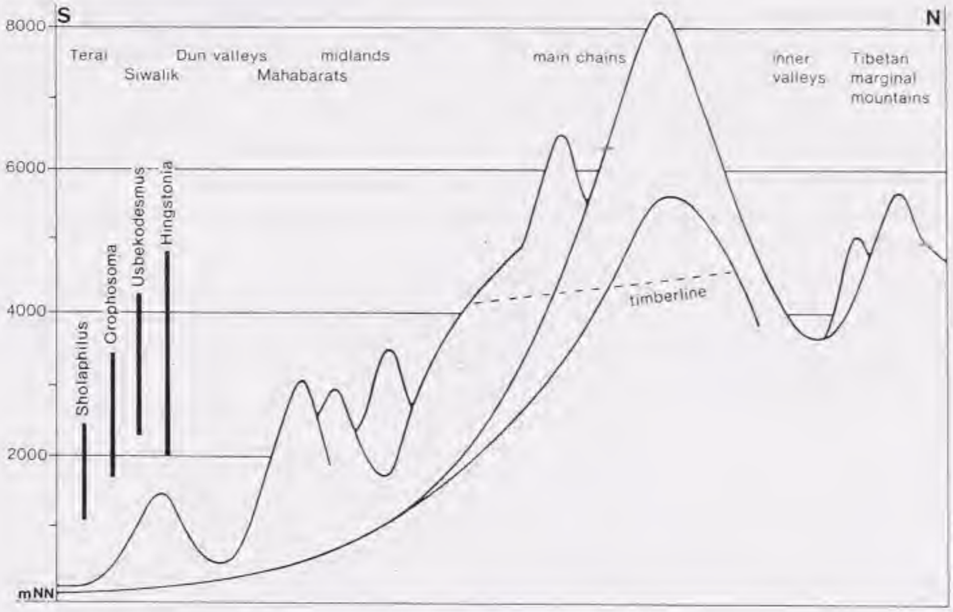


FIG. 3. — Vertical distribution of some millipede genera in the Central Himalayas - genera *Usbekodesmus*, *Hingstonia*, *Sholaphilus*, *Orophosoma*.

From the primary immigration routes of invertebrate and vertebrate faunal components in the Central Himalayas, MARTENS (1984, 1993) distinguished Central Asian, West Asian Himalayan, Tropical Indian, West Chinese Himalayan, and Indochinese Himalayan pathways (Fig. 4). However, because of their preponderance in forests, only two major dispersal routes are available to the Diplopoda, from Southeast Asia and the Indian subcontinent. Consequently, the millipede fauna of the Central Himalayas is dominated by such tropical elements as the families Sphaeropoeidae, Siphonophoridae, Andrognathidae, Harpagophoridae, Cambalopsidae, Physobolidae, Cryptodesmidae, Opisotretidae, Fuhrmannodesmidae, Paradoxosomatidae, Pyrgodesmidae, etc., which have Oriental and/or Indian affinities. In the relatively well-explored Central Himalayas, most millipede species are restricted to tropical lowland forests such that it is difficult to discriminate Southeast from Indian derivatives. Possibly only *Sholaphilus*, *Trichopeltis* and certain Sphaeropoeidae hold eutropical Indian origins.

Source : MNHN, Paris

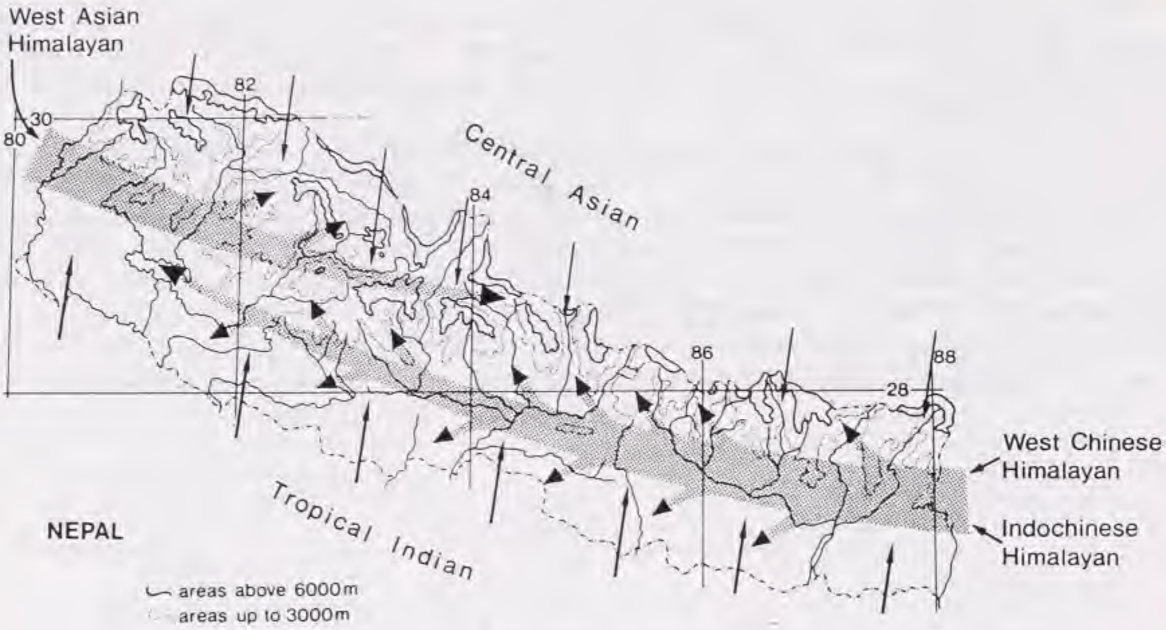


FIG. 4. —The main immigration routes of faunal components into the Nepal Himalayas.

Such genera as *Hyleoglomeris*, *Tianella*, *Anaulaciulus*, and *Usbekodesmus* are primarly Palearctic and are restricted in the Central Himalayas to the uppermost forests, some even spreading into alpine meadows above 4,000 m a.s.l., which contrasts with nearly 6,000 m for certain other terrestrial invertebrates, e.g. spiders (MARTENS, 1993). The highest millipede record in the Himalayas, and probably also in the world, is of *Nepalmatoiulus ivanloebli* (ENGHOFF, 1987) encountered at 4,800 m a.s.l. Other millipedes demonstrate subtropical east and southeast Asian elements, although there are occasional exceptions to the general rule, "(sub)tropical creatures in (sub)tropical environments only". Families that are more subtropical than tropical include the Kashmireumatidae (with the oligotypic genus, *Kashmireuma*, in the Himalayas and another monobasic genus in Vietnam), Megalotylidae (with the Oriental genus *Nepalella* and a monobasic genus in the Russian Far East), Julidae (with *Anaulaciulus* and the Oriental highly prolific genus *Nepalmatoiulus*), and certain Fuhrmannodesmidae and Paradoxosomatidae [e.g., the endemic genera *Hingstonia* and *Orophosoma* (Fig. 3)].

The border between subtropical and purely tropical Himalayan components seems to be vague (MARTENS, 1984, 1987b, 1993), as is that between forest (sub)zones (Fig. 2). Only a few genera and even fewer tribes and families display clear vertical distribution patterns. In most species there are only slight correlations with particular elevations. Some closely related genera and species tend to occupy different altitudinal zones, probably because of niche segregation. For example, *Hingstonia* and *Sholaphilus* (Fuhrmannodesmidae) tend to inhabit upper and lower forests, respectively (Fig. 3), and this pattern is better demonstrated within speciose genera. *Usbekodesmus*, for example, tends to be restricted to the upper forest belt, but a few components are confined to low elevations, between 2,300 and 4,250 m a.s.l. (Table 1, Fig. 3).

The same patterns have been reported for spiders, harvestmen, insects, birds, etc. (MARTENS, 1984, 1987b, 1993), but the Diplopoda is distinguished in being almost strictly sylvicolous and virtually entirely Oriental and/or Indian in origin.

The classical pattern of a prolonged cis-Himalayan band west of Brahmaputra, marking the northwesternmost border of the Oriental realm, is highly characteristic of Oriental Diplopoda

Source : MNHN, Paris

(HOFFMAN & BURKHALTER, 1978), and most Himalayan genera and tribes demonstrate this pattern. An Oriental influence dominates in Kashmir, which is the classics, but also, unexpectedly, to the north beyond the Indus Valley. Thus, judging from millipedes "...the less elevated and more mild areas of modern North Pakistan seem to have retained particularly ancient faunal elements as compared to the adjacent extremely high and severe Himalayas nowadays supporting only relatively more advanced, younger forms" (GOLOVATCH, 1991a: 876).

FAUNOGENESIS

As the regional phyto- and paleogeography are well documented (WULFF, 1944; MEYEN, 1987), one can reasonably surmise that the Himalayas have served as a dispersal pathway for a uniform Turgai biota (e.g. *Quercus*, *Pyrus*, *Malus*, and deciduous tree genera and associated faunas) during the early and mid-Tertiary, which spread northwestward along the receding southern coast of the Tethys Sea. A very considerable proportion of present-day European and Mediterranean millipede genera, tribes, and families also seem to reflect repeated northwestward dispersals from source areas in East and/or Southeast Asia, for example *Hyleoglomeris* and possibly the Glomeridae as a whole, the tribes Brachyiulini and Leucogeorgiini (Julidae), the tribe Paradoxosomatini and possibly all Paradoxosomatidae, and the genus *Polydesmus* and possibly all Polydesmidae (GOLOVATCH, 1987, 1991a, 1991b, 1993).

Beyond their effects on areas to the northwest, the Himalayas have also been a center of secondary diversification since the Plio-Pleistocene, and much of the Central and West Himalayas seem to have experienced a pronounced, secondary faunal impoverishment (GOLOVATCH, 1991a), because all endemic millipedes display a relatively low taxonomic rank. The development of local species swarms (among *Tianella*, *Nepalella*, *Anaulaciulus*, *Nepalmatoiulus*, *Gonoplectus*, *Hingstonia*, *Himalodesmus*, *Paranedyopus*, etc.) through allopatric speciation is a prominent characteristic of Himalayan Diplopoda irrespective of origin, as has been observed among other soil/litter arthropods (MARTENS, 1987b, 1993). The few anthropochorous introductions are very recent and have failed to alter the general zoogeographic pattern of Himalayan Diplopoda.

Although preliminary, these reconstructions provide a basis for comparisons for future faunistic and zoogeographic studies of the Himalayas. Compared to other terrestrial Arthropoda (MARTENS, 1993), the salient aspects of Himalayan Diplopoda are pronounced sylvicoly and Oriental and/or Indian origin, and their ostensible Palearctic influence also originates in present-day subtropical regions of Southeast and East Asia.

REFERENCES

DOBREMEZ, J. F., 1972. — Les grandes divisions phytogéographiques du Népal et de l'Himalaya. *Bull. Soc. bot. France*, **119** : 111-120.

GOLOVATCH, S. I., 1987. — The *alluaudi*-group of *Glomeris*, another Macaronesian species swarm in millipedes (Diplopoda: Glomeridae). *Entomol. scand.*, **17** : 503-509.

GOLOVATCH, S. I., 1990. — Diplopoda from the Nepal Himalayas. Several additional Polydesmidae and Fuhrmannodesmidae (Polydesmida). *Spixiana*, **13** : 237-252.

GOLOVATCH, S. I., 1991a. — On a small collection of millipedes (Diplopoda) from northern Pakistan and its zoogeographic significance. *Rev. suisse Zool.*, **98** : 865-878.

GOLOVATCH, S. I., 1991b. — The millipede family Polydesmidae in Southeast Asia, with notes on phylogeny (Diplopoda: Polydesmida). *Steenstrupia*, **17** : 141-159.

GOLOVATCH, S. I., 1993. — On several new or poorly-known Oriental Paradoxosomatidae (Diplopoda, Polydesmida). *Arthropoda Selecta*, **2** : 3-14.

HOFFMAN, R. L., 1980. — *Classification of the Diplopoda*. Genève, Mus. Hist. nat., (1979) 237 pp.

HOFFMAN, R. L. & BURKHALTER, E. A., 1978. — Studies on spirostreptoid millipeds XIV. A new species of *Gonoplectus* from Thailand, with notes on the status and distribution of the genus (Spirostreptida: Harpagophoridae). *J. nat. Hist.*, **12** : 413-422.

Source : MNHN, Paris

KORSÓS, Z., 1996. — Another Himalayan group of julid millipedes: Towards the clarification of the genus *Anaulaciulus* Pocock, 1895 (Diplopoda, Julida). *Senckenberg. biol.* (in press).

MARTENS, J., 1984. — Vertical distribution of Palaearctic and Oriental faunal components in the Nepal Himalayas. *Erdwissenschaftl. Forsch.*, **18** : 321-336.

MARTENS, J., 1987a. — Remarks on my Himalayan expeditions. *Courier Forsch.-Inst. Senckenberg*, **93** : 7-31.

MARTENS, J., 1987b. — Beiträge zur Fauna, Faunengenese und Zoogeographie des Nepal-Himalaya. Arthropoda. *Cour. Forsch.-Inst. Senckenberg*, **93** : 503 pp.

MARTENS, J., 1993. — Bodenlebende Arthropoda im zentralen Himalaya: Bestandsaufnahme, Wege zur Vielfalt und ökologische Nischen. *Erdkundliches Wissen*, **112** : 231-249.

MASCLE, G., DELCAILLAU, B. & HERAIL, G., 1990. — La formation de l'Himalaya. *La Recherche*, **217** : 30-39.

MEYEN, S. V., 1987. — *Foundations of paleobotany*. Moscow, "Nedra" Publrs, 403 pp. [In Russian].

TROLL, C., 1967. — Die klimatische und vegetationsgeographische Gliederung des Himalaya-Systems. *Khumbu Himal*, **1** : 353-388.

WULFF, E. V., 1944. — *Historical geography of plants. The history of the world's floras.* Moscow-Leningrad, Akad. Nauk SSSR Publrs, 546 pp. [In Russian].

Source : MNHN, Paris

Étude systématique et écologique des myriapodes dans le Parc National de Chréa (Atlas blidéen), Algérie

Ourida ***ABROUS-KHERBOUCHE***

Université des Sciences et de la Technologie Houari Boumédienne, I.S.N. Lab. d'écologie animale
B.P. 32 El Alia Bab Ezzouar Alger, Algérie

RÉSUMÉ

Les Myriapodes, notamment les diplopodes, jouent un rôle important dans la fragmentation de la litière et les premières étapes du recyclage des minéraux dans le sol. Peu d'études ont été consacrées à ces groupes fonctionnels d'arthropodes en Algérie. Pour cela, nous nous sommes proposés d'étudier les myriapodes (Diplopoda & Chilopoda) de sept stations situées sur un gradient altitudinal dans le Parc National de Chréa (Atlas de Blida), plus particulièrement sur les djebels Chréa et Mouzaïa, séparés par le profond ravin de l'oued Chiffa. Un premier résultat consiste en la liste faunistique de toutes les espèces récoltées : 14 espèces appartenant à 7 ordres différents sont répertoriées. L'étude autécologique des espèces les plus abondantes permet de préciser leurs préférences biotiques et leur abondance relative au sein de chacun des milieux qui sont largement décrits dans ce travail. L'étude comparative des peuplements montre que la richesse spécifique ainsi que l'abondance relative augmentent généralement avec l'altitude. L'une et l'autre sont plus élevées sur le djebel Chréa que sur le djebel Mouzaïa. En outre, à l'aide du coefficient cœnotique de JACCARD, nous constatons l'existence de deux groupes distincts dans les stations d'étude.

ABSTRACT

Systematic and ecological study of Myriapod communities in the Chrea National Park (Blida Atlas, Algeria).

Myriapoda - particularly Diplopoda - play an important role in litter-breakdown and soil mineralisation. Very few studies have dealt with their ecological role in Algerian ecosystems. Hence it was decided to investigate millipede and centipede populations in seven study sites ranging along an altitudinal gradient in the Chrea National Park (Blida Atlas), precisely on Chrea djebel and Mouzaïa djebel, which are divided by the deep canyon of oued Chiffa. The first result is a check-list of all species collected at these sites: 14 species belonging to 7 different orders have been identified. The ecological study of the most abundant species shows their biotic preferences and phenology. Following population sampling, we can observe an increase in species richness and abundance related to altitude. Both are greater on Chrea djebel than on Mouzaïa djebel. Using the JACCARD coefficient, we recognize two distinct groups in the different study sites.

INTRODUCTION

Dans toute étude écologique, relative notamment à l'organisation des peuplements, la systématique et la taxinomie sont de plus en plus indispensables ; sans elles, la comparaison des biotopes et la connaissance précise de la structure des peuplements sont totalement impossibles ou présentent un risque d'erreur d'interprétation majeur.

ABROUS - KHERBOUCHE, O., 1996. — Étude systématique et écologique des myriapodes dans le Parc National de Chréa (Atlas blidéen), Algérie. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 175-186. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

Très peu d'études à ce jour ont été consacrées aux myriapodes dans les écosytèmes naturels algériens. Ces animaux y jouent toutefois un rôle important, soit dans la fragmentation de la litière et le transfert ou le recyclage de la matière minérale et organique (Diplopodes), soit dans les processus de régulation des populations-proies de micro- ou de mésoarthropodes du sol (Chilopodes).

C'est en 1840 qu'une première approche myriapodologique a été entreprise par BRANDT sur la région d'Alger, puis LUCAS (1846) a étudié une large partie de la faune myriapodologique Nord Africaine.

Par la suite, BRÖLEMANN (1897, 1925, 1930, 1931) a approfondi les recherches myriapodologiques du point de vue de leur taxinomie et de leur répartition au sein de diverses entités écologiques. En 1921, il signala 38 espèces de diplopodes en Algérie, 23 en Tunisie, 4 au Maroc et une espèce en Lybie. Nous donnons dans ce travail la description des milieux d'étude qui ont servi à une approche comparative de l'organisation des peuplements de chilopodes et de diplopodes, dont les premiers résultats sont exploités et discutés.

MATÉRIEL ET MÉTHODES

Dix pièges d'interception de type BARBER ont été utilisés dans chaque station pour capturer les myriapodes du Parc National de Chréa. Ils ont été relevés mensuellement durant la période de Janvier 1989 à Septembre 1990.

Du fait de problèmes techniques, la période de récolte n'a pas été rigoureusement régulière pour toutes les stations. Pour les études comparatives, seule la période de Juin 1989 à Juin 1990 a été prise en considération.

L'identification du matériel a été rendue trés difficile à cause de l'ancienneté de la littérature et par le fait que plusieurs espèces étaient inconnues ou de statut incertain. Nous avons bénéficié de l'aide du Dr. SERRA, de l'Université de Barcelone (Espagne) et de J.-P. MAURIÈS,du Muséum National d'Histoire Naturelle de Paris (France) respectivement pour la vérification des espèces de chilopodes et de diplopodes.

PRÉSENTATION DES MILIEUX

Le Parc National de Chréa est l'un des 9 parcs nationaux que compte aujourd'hui l'Algérie. D'une superficie de 26000 ha, il s'étend sur les versants Nord et Sud de l'Atlas Blidéen, qui appartient à l'Atlas Tellien. Ce parc entoure le village de Chréa et englobe les djebel s Guerroumen, Ferroukha et Mouzaia. Les deux premiers sont séparés du dernier par le ravin de l'oued Chiffa (Fig.1).

D'après HALIMI (1980), le climat du parc varie entre humide-doux sur les versants les plus bas et humide-frais sur les versants plus élevés et les sommets. La formation végétale la plus caractéristique du Parc est la Cédraie, à partir de 1100 m sur le djébel Guerroumen. Le djébel Ferroukha est couvert d'une forêt dégradée de *Quercus ilex*. En dessous de 1000-1100 m, nous rencontrons des forêts de *Pinus halepensis*, *Quercus ilex* ou *Quercus faginea*. Sur le djebel Mouzaia, la Cédraie est absente. Elle est remplacée par des chênaies mélangées de forêts de *Olea europea.* Pour étudier les myriapodes du Parc National de Chréa, sept stations situées sur un gradient altitudinal ont été choisies.

a) La station Roseaux

- Altitude et localisation : cette station est située à 185 m d'altitude sur le djebel Mouzaia et à quelques mètres de l'oued Chiffa (Fig. 1).

- Exposition et étage bioclimatique : elle est à exposition Nord-Est et se localise dans l'étage bioclimatique sub-humide à hiver légèrement chaud (Fig. 2).

- Composition floristique et caractéristiques pédologiques : la station Roseaux se caractérise par l'absence de strate arborescente. Elle présente une strate arbustive assez dense mais peu diversifiée. *Phragmites australis* et *Laurus roseus* sont les seules espèces herbacées, avec un recouvrement variant de 60 à 70%. Le sol de cette station est tapissé d'une litière peu épaisse, formée essentiellement d'herbes. Le pH est égal à 6,7 et l'humidité à 37%.

Source : MNHN, Paris

b) La station Broussaille riveraine

Altitude et localisation : elle est située à 300 m sur le djebel Mouzaia, le long de la route Nationale n°1, à côté d'un petit affluent permanent de l'oued Chiffa, à quelques dizaines de mètres de la vallée de l'oued Chiffa.

Exposition et étage bioclimatique : la station Broussaille riveraine est à exposition Nord-Est. Elle est localisée dans l'étage bioclimatique sub-humide et sous étage doux (Fig. 2).

Composition floristique et caractéristiques pédologiques : la végétation est composée essentiellement de trois strates :

1) La strate arborescente à un recouvrement moyen de 40 à 45%, avec *Salix alba* comme seul représentant.

2) La strate arbustive comprend 9 espèces et recouvre 30 à 40%. *Ficus carica, Olea europea et Rosa semperviens* sont les espèces abondantes.

3) La strate herbacée est très dense, constituée de plusieurs espèces et présente une litière plus ou moins compacte, composée d'herbes et de quelques feuilles, les herbes atteignant 40 cm. Le sol de cette station présente un pH = 6,7 et une humidité de 35%.

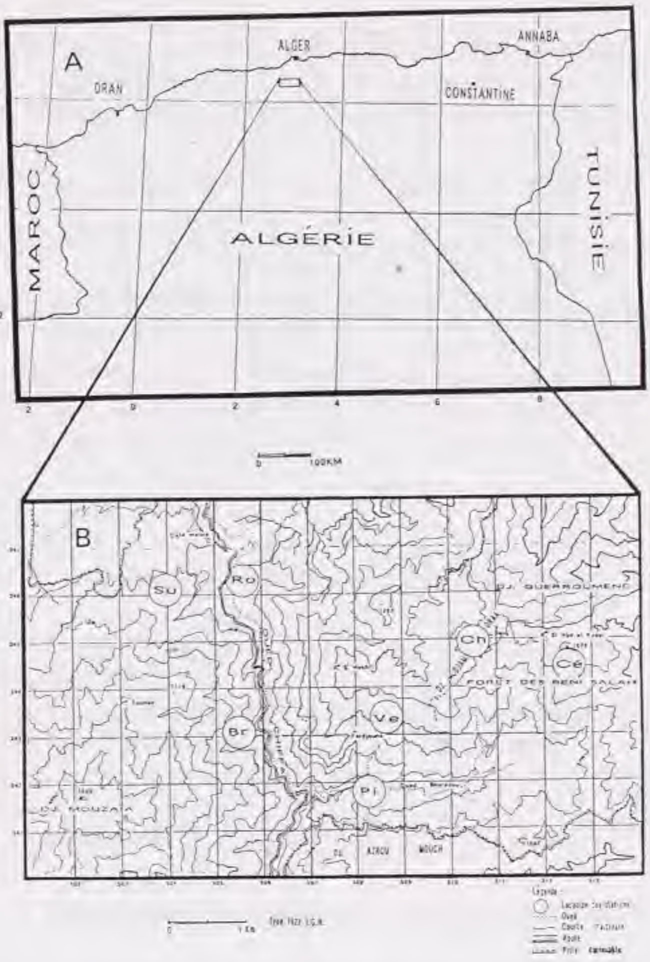


FIG. 1. — Localisation de l'Atlas blidéen (A) et des stations (B). Ro : Roseaux, Br : Broussaille riveraine, Su : Subéraie, Pi : Pinède, Ve : Verger, Ch : Chênaie, Ce : Cédraie.

FIG. 1. — Localization of the Blidean Atlas and of the study sites. Ro: reeds, Br: Riverside brushwood, Su: Oak-wood (Q. suber), Pi: Pine-wood, Ve: Orchard, Ch: Oak-wood (Q. ilex), Ce: Cedar-wood.

c) La station Pinède

Altitude et localisation : la Pinède est située à 400 m sur le djebel Chréa, au Sud du village Fordjouna, le long de l'oued Bouredou qui est un affluent de l'oued Chiffa.

Exposition et étage bioclimatique : la station est exposée au Nord-Nord-Est ; elle est située dans l'étage bioclimatique sub-humide à hiver doux (Fig. 2).

Composition floristique et caractéristiques pédologiques : la végétation est répartie sur trois strates :

1) La strate arborescente : *Pinus halepensis* est l'espèce dominante avec un recouvrement de 30 à 40%. Il peut atteindre une hauteur de 12 à 13 m.

2) La strate arbustive est dense et constituée de 9 espèces. *Pistachia lentiscus,* l'espèce dominante, et *Erica arborea,* espèce abondante, atteignent une hauteur de 12 m.

3) La strate herbacée, avec 11 espèces, présente un recouvrement de 30 à 40%. *Acanthus maulus* est l'espèce la plus abondante. Le substrat est représenté par un sol à pH = 6.6 ; il est recouvert d'une litière peu épaisse, formée essentiellement de feuilles de *Pinus halepensis*. La présence de mousse est indicatrice d'une humidité du sol un peu plus forte, égale à 39%.

Source : MNHN, Paris

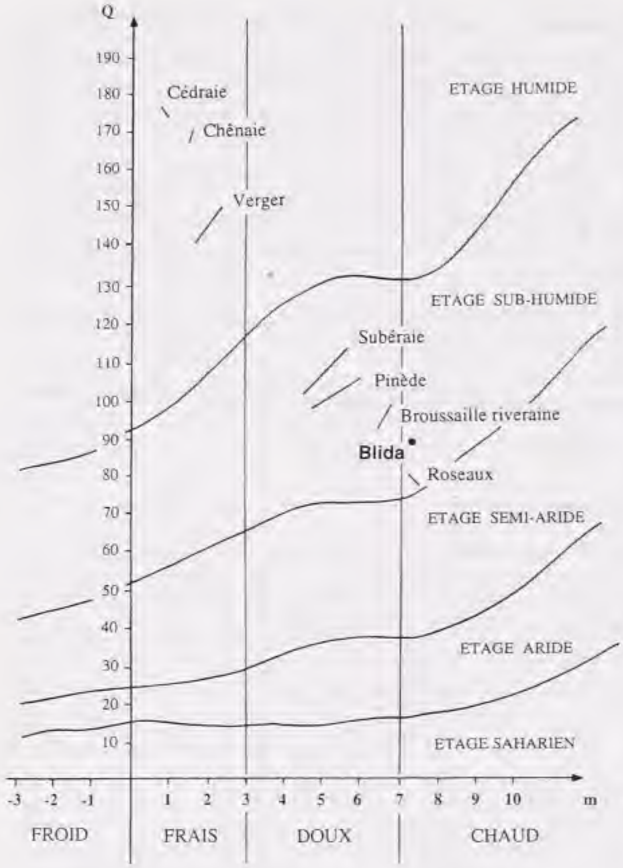


FIG. 2. — Les étages bioclimatiques des stations étudiés dans l'Atlas blidéen.

FIG. 2. — Bioclimatic stages of the study site in the Blidean Atlas.

d) La station Subéraie

Altitude et localisation : Elle est située à 450 m sur le djebel de Mouzaia, au Sud-Ouest du lieu dit "Café maure" (Fig. 1).

Exposition et étage bioclimatique : la Subéraie est à exposition Sud-Est et se localise dans l'étage bioclimatique sub-humide doux.

Composition floristique et caractéristiques pédologiques :

1) la strate arborescente dominée par *Quercus suber* , présente un recouvrement inférieur à celui de la pinède.

2) la strate arbustive, avec ses sept espèces, présente un recouvrement de 70 à 80%. *Pistachia lentiscus* domine, *Erica arborea* et *Olea europea* sont abondants.

3) le recouvrement de la strate herbacée est en moyenne de 50 à 60 %. Les espèces les plus fréquentes sont *Ranunculus spicatus* et diverses Graminés.

Durant la période d'étude, cette station présentait une végétation sèche. La litière, essentiellement composée de feuilles sèches de *Quercus ilex, Pistachia lentiscus*, de branches et bourgeons morts ainsi que de feuilles-épines de *Calycotome spinosa*, présente une humidité du sol faible (20%) par rapport aux autres stations. Le pH est en revanche plus élevé que dans les stations précèdentes (7,1).

e) La station Verger

Altitude et localisation : cette station est située à 1000 m sur le djebel Chréa à quelques centaines de mètres du village Fourdjouna.

Exposition et étage bioclimatique : elle est exposée au Sud-Sud-Ouest et se situe dans l'étage bioclimatique humide et sous-étage frais.

Composition floristique et caractéristiques pédologiques : la végétation de cette station comporte trois strates :

1) la strate arborescente : le recouvrement faible varie entre 10 et 20%. *Cerasus avium* est la seule espèce abondante, sa hauteur ne dépasse pas 4 m.

2) la strate arbustive comprend quelques espèces rares. *Erica arborea*, fréquente, ne dépasse pas 1,5 m. Le recouvrement est de 50 à 60%.

3) la strate herbacée : elle est dense avec beaucoup d'espèces qui recouvrent 90 à 95%. Le sol, à pH = 6,7 et humidité = 33%, est recouvert d'une litière épaisse de 3 à 4 cm, composée de feuilles de *Cerasus avium, Pyrus communis, Malus mitis* ainsi que d'herbes et de quelques branches.

Source : MNHN, Paris

f) La station Chênaie

Altitude et localisation : elle se trouve à 1400 m sur le djebel Chréa (Mont Djamaa Draa) à 1400 m d'altitude, dans la forêt de Béni Salah.

Exposition et étage bioclimatique : la Chênaie, à exposition Sud-Ouest, est située dans l'étage bioclimatique humide à hiver frais.

Composition floristique et caractéristiques pédologiques : la végétation de la station est composée des strates suivantes :

1) la strate arborescente : le recouvrement est de 20 à 30% avec *Quercus ilex* comme seul représentant.

2) la strate arbustive : avec trois espèces recouvrant 90 à 95%, *Quercus ilex* est dominant.

3) la strate herbacée : le recouvrement est de 80%. *Calycotome spinosa* est l'espèce dominante. Le sol rocheux de cette station, constitué de schiste, est tapissé par une litière de 3 à 4 cm d'épaisseur, formée essentiellement par des feuilles de chêne-vert (*Quercus ilex*) et quelques feuilles de *Cistus monspeliensis.* Le pH est identique à celui de la station Verger (6,7) mais l'humidité est plus faible (33%).

g) La station Cédraie

Altitude et localisation : elle est située à 1600 m dans la forêt de Béni Salah à 29 m du pic dit "Koudia Sidi Abdelkader" (1629 m).

Exposition et étage bioclimatique : La station Cédraie est à exposition Sud-Ouest et est située dans l'étage bioclimatique humide et sous étage frais (Fig. 2).

Composition floristique et caractéristiques pédologiques : cette station présente une formation arborescente assez dense, formée uniquement de cèdres (*Cedrus atlantica*), d'une hauteur moyenne de 5 à 18 m. Nous y retrouvons les trois strates végétales :

1) la strate arborescente : la hauteur et la densité de ces arbres (*Cedrus atlantica)* empêchent les rayons du soleil d'atteindre le sol : les autres strates présentent un recouvrement moins important.

2) la strate arbustive : *Cedrus atlantica* est la seule espèce rare avec un recouvrement de 20 à 30%.

3) la strate herbacée : contient un nombre d'espèces plus élevé que les autres stations ; parmi les 17 espèces relevées, *Chrysantemum segetum, Graminea* sp. et *Ranunculus spicatus* sont les plus fréquentes.

Le sol de cette station est recouvert d'une litière de 2 à 3 cm et plus dans certains endroits. Elle est composée essentiellement d'aiguilles de cèdre, de branches et de nombreux rameaux morts. Le sol a un pH neutre (6,7) et son humidité est égale à 33%.

RÉSULTATS ET DISCUSSION

Dans le Parc National de Chréa, nous avons récolté 14 espèces appartenant à 7 ordres différents (Tableau 1). Le nombre d'espèces dans les ordres Geophilomorpha et Lithobiomorpha et le nombre d'individus des espèces de Julida (Iuliformia) et Polydesmida sont les plus élevés.

Le Tableau 2 montre que la richesse spécifique des diplopodes est très faible dans les deux premières stations (Roseaux, 185 m et Broussaille riveraine, 300 m d'altitude). En revanche, ils sont plus abondants dans les stations de haute altitude (Verger, Chênaie et Cédraie).

Les Chilopodes se rencontrent dans la majorité des stations. Roseaux, Pinède et Subéraie présentent toutefois un faible effectif.

Sur le diagramme (Fig. 3), nous remarquons l'absence de l'ordre Scutigeromorpha dans la station Roseaux (185 m) située à quelques mètres de l'oued Chiffa, et qui semble être un milieu défavorable. L'ordre Scolopendromorpha n'est présent que dans la Chênaie (1400 m) ; il semble préférer les stations homogènes avec une litière épaisse, formée de feuilles sèches, de branches et de bourgeons morts.

Source : MNHN, Paris

TABLEAU 1. — Nombre d'espèces et d'individus capturés, par ordre, dans le Parc National de Chréa (Atlas blidéen).
TABLE 1. — Number of species and individuals collected per order in the Parc National de Chréa (Blidean Atlas).

Classes	Ordres	Nbre d'espèces	Nbre d'individus
	Julida	2	329
DIPLOPODA	Polydesmida	2	211
	Glomerida	1	23
	Geophilomorpha	3	66
CHILOPODA	Lithobiomorpha	4	89
	Scolopendromorpha	1	2
	Scutigeromorpha	1	58
Total		14	778

TABLEAU 2. — Liste des espèces de diplopodes et chilopodes capturés et leur abondance dans les stations étudiées. Ro : Roseaux, Br : Broussaille riveraine, Su : Subéraie, Pi : Pinède, Ve : Verger, Ch : Chênaie, Ce : Cédraie. Tot = nombre total d'individus.

TABLE 2. — Check-list of millipedes and centipedes, relative abundance in the study sites. Ro: reeds, Br: Riverside brushwood, Su: Oak-wood (Q. suber)*, Pi: Pine-wood, Ve: Orchard, Ch: Oak-wood* (Q. ilex)*, Ce: Cedar-wood. Tot = total number of individuals.*

Ordres	Espèces	Ro	Br	Pi	Su	Ve	Ch	Ce	Tot
Julida	*Ommatoiulus gauthieri*	0	0	3	11	62	6	3	85
	Phalloiulus distinctus	0	0	13	3	1	45	182	244
Glomerida	*Glomeris conspersa*	1	0	11	0	1	10	0	23
	Polydesmus superus	1	2	0	0	0	0	0	3
Polydesmida	*Archipolydesmus* sp.	0	0	5	0	0	2	201	208
	Geophilus carpophagus	0	10	0	0	7	4	18	39
	Geophilus sp.	0	3	0	0	0	0	14	17
Geophilomorpha	*Schendyla* sp.	0	2	0	0	0	0	8	10
	Lithobius crassipes	0	0	0	0	5	19	1	25
	Lithobius castaneus	4	1	2	2	10	9	19	47
Lithobiomorpha	*Lithobius* sp.	2	9	1	0	0	0	3	15
	Lithobius forficatus	1	0	0	0	1	0	0	2
Scolopendromorpha	*Scolopendra* sp.	0	0	0	0	0	2	0	2
Scutigeromorpha	*Scutigera coleoptrata*	0	16	7	10	19	1	5	58

L'étude synécologique montre que la richesse spécifique ainsi que le nombre d'individus augmentent généralement avec l'altitude (Fig. 4). La Subéraie (450 m) présente le nombre d'espèces le plus faible. Ceci peut être dû à la faible humidité du sol (20,40) de cette station.

Le dendrogramme obtenu à l'aide du coefficient cœnotique de JACCARD révèle l'existence de deux groupes distincts de stations ayant une similarité de 12,50 % (Fig. 5).

La station Verger (1000 m) et la Chênaie (1400 m) présentent la similarité la plus élevée (69,85%), suivies par la Cédraie (1600 m), avec laquelle elles forment un premier groupe. Ce sont des stations relativement humides situées sur le même djebel Chréa et à exposition sud-ouest.

Le second groupe rassemble quatre stations : la Subéraie, la Pinède, la Broussaille riveraine et la station Roseaux.

La Subéraie et la Pinède, situées respectivement à 450 m et 400 m d'altitude, sont des stations sub-humides, homogènes, qui présentent la similarité la plus élevée (43,60%). Elles offrent des conditions climatiques très voisines et, par conséquent, des microclimats similaires.

Source : MNHN, Paris

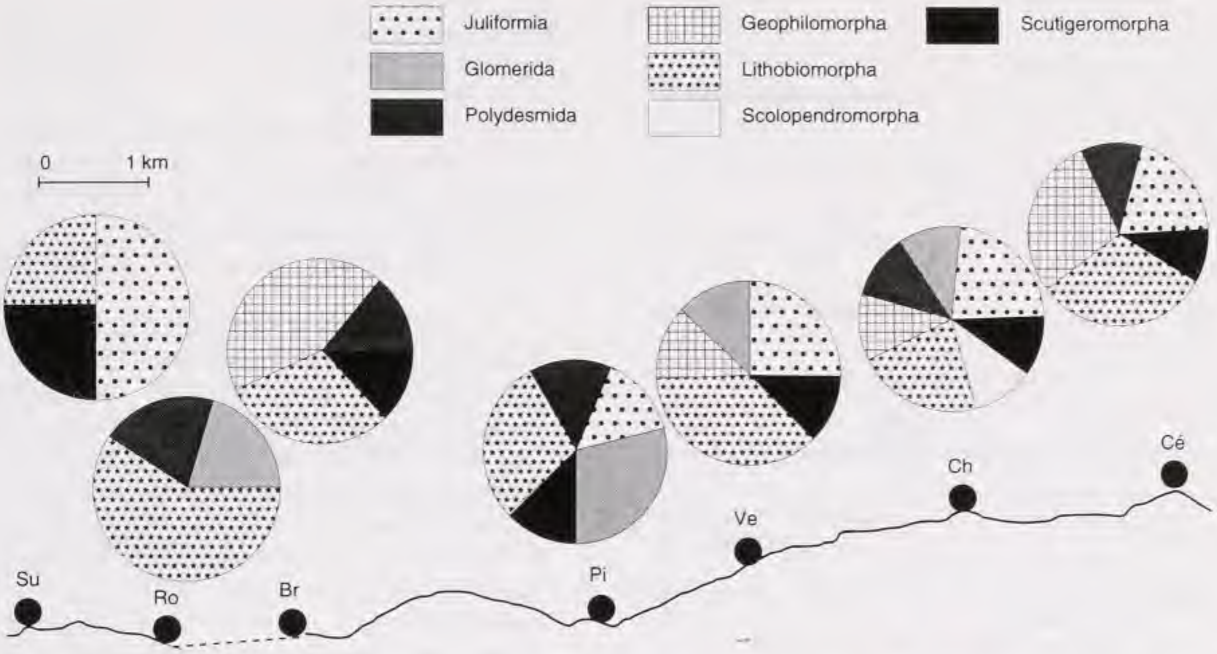


FIG. 3. — Diagramme représentant les proportions du nombre d'espèces pour les différents ordres dans les stations étudiées. Ro : Roseaux, Br : Broussaille riveraine, Su : Subéraie, Pi : Pinède, Ve : Verger, Ch : Chênaie, Ce : Cédraie.

*FIG. 3. — Relative importance of the specific richness for the different orders in the study sites. Ro: Reeds, Br: Riverside brushwood, Su: Oak-wood (*Q. suber*), Pi: Pine-wood, Ve: Orchard, Ch: Oak-wood (*Q. ilex*), Ce: Cedar-wood.*

FIG. 4. — Nombre d'espèces et d'individus capturés par station dans le Parc National de Chréa (Atlas blidéen).

FIG. 4. — Number of species and individuals in each site in the Parc National de Chréa.

Source : MNHN, Paris

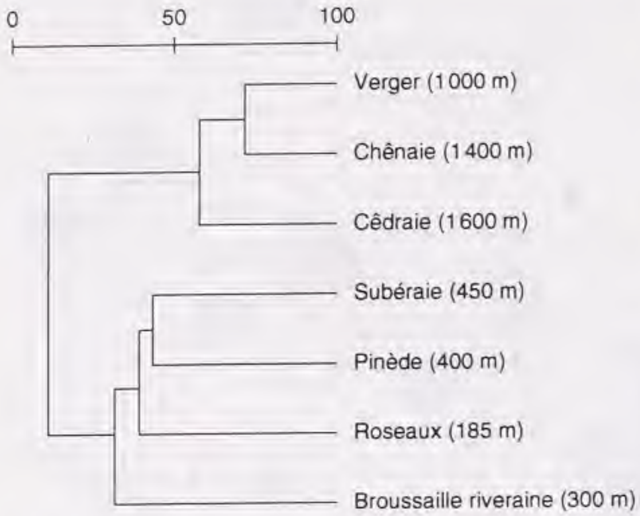


FIG. 5. — Dendogramme de similitudes des stations étudiés dans l'Atlas blidéen.
FIG. 5. — Similarities between the study sites.

A ces deux stations s'ajoute la station Roseaux (185 m) et enfin, la Broussaille riveraine (300 m) avec une similarité de 32,9 %.

L'étude autoécologique de 3 espèces dont l'abondance relative est importante permet d'indiquer leurs préférences écologiques et leurs phénologies :

Ommatoiulus gauthieri (Brolemann, 1931)

Cette espèce a été décrite du djebel Bouzegza par BROLEMANN (1931). Elle présente une très grande variabilité morphologique. Dans l'Atlas blidéen, nous l'avons récoltée dans presque tous les sites d'étude. Elle est absente seulement dans les stations Roseaux et Broussaille. Le plus grand nombre d'individus (62) a été récolté dans la station Verger (1000 m). Cette espèce semble préférer une végétation dense avec une litière composée de feuilles et d'herbes.

Les mâles ont été récoltés durant l'été, l'automne et l'hiver. Ils montrent une activité intense à la fin de l'automne et au début de l'hiver (Fig. 6). Les femelles sont plus actives au début de l'automne et se rencontrent elles aussi, durant l'été, l'automne et l'hiver.

Cylindroiulus (= Phalloiulus) distinctus (Lucas, 1846)

Cet iulide a été signalé dans les bois de Boulogne près d'Alger par BROLEMANN en 1931; à l'exception de la station Roseaux (185 m), elle se retrouve dans toutes les autres stations. Le plus grand effectif (182 individus) a été trouvé dans la Cédraie, ce qui laisse supposer une préférence pour les hautes altitudes, avec une litière composée essentiellement d'aiguilles de *Cedrus atlantica*. Les individus de cette espèce ont été récoltés en toute saison (Fig. 7) mais, le plus grand nombre a été capturé à la fin de l'automne et au début de l'hiver.

Archipolydesmus sp.

Cette espèce qui, d'après J.-P. MAURIÈS (Muséum N. H. N., Paris) est polymorphe, nouvelle et appartient à un genre inédit en Algérie, a été récoltée dans la Pinède, la Chênaie, la Cédraie et la station Broussaille, elle est absente dans les autres sites. Toutefois, là où elle est présente, l'effectif demeure faible. C'est dans la Cédraie (1600 m) que l'on observe l'effectif le plus élevé (201 individus). Ceci montre que cette espèce préfère les hautes altitudes avec une humidité atmosphérique relativement grande. Comme le montre la Figure 8, les mâles et les femelles de cette espèce ont été capturés de l'automne jusqu'à la fin du printemps. Ils sont très actifs pendant l'automne et le début de l'hiver.

CONCLUSION

Cette étude préliminaire relative aux myriapodes du Parc National de Chréa apporte une contribution à une meilleure connaissance de la faune algérienne, en réunissant les données initiales d'une approche de l'organisation des peuplements de chilopodes et de diplopodes au sein de plusieurs types d'écosystèmes nord-africains typiques.

Bien que demeurant faibles en général, le nombre d'espèces ainsi que le nombre d'individus augmentent avec l'altitude : la station culminante (Cédraie, 1600 m) présente la plus grande richesse spécifique et la plus grande abondance (10 espèces et 440 individus capturés).

Source : MNHN, Paris

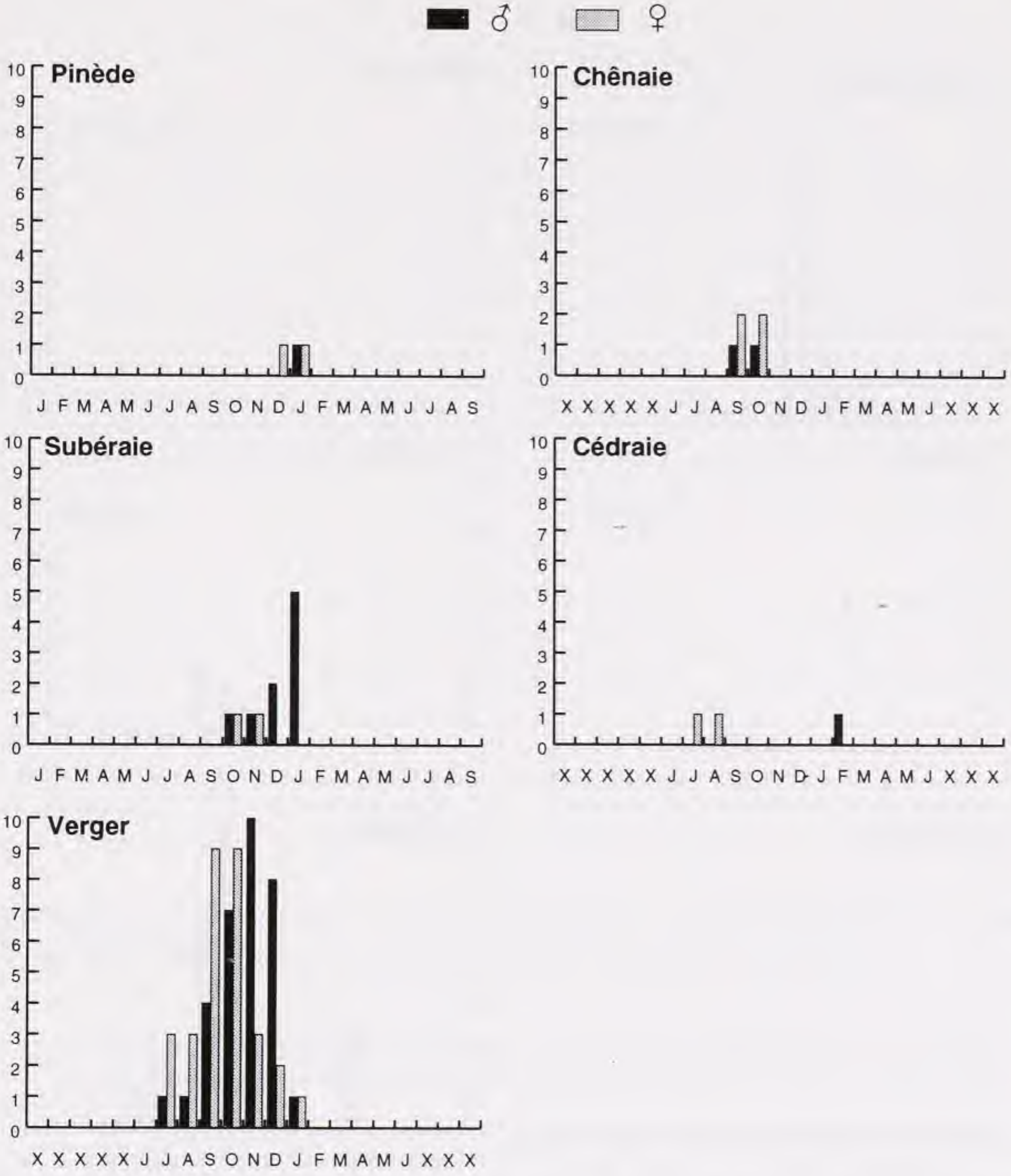


FIG. 6. — Abondance et activité relatives mensuelles de *Ommatoiulus gauthieri* dans les stations étudiées (x = période non échantillonnée).

FIG. 6. — Relative abundance and activity of Ommatoiulus gauthieri *in the study sites (x = no sampling).*

Source : MNHN, Paris

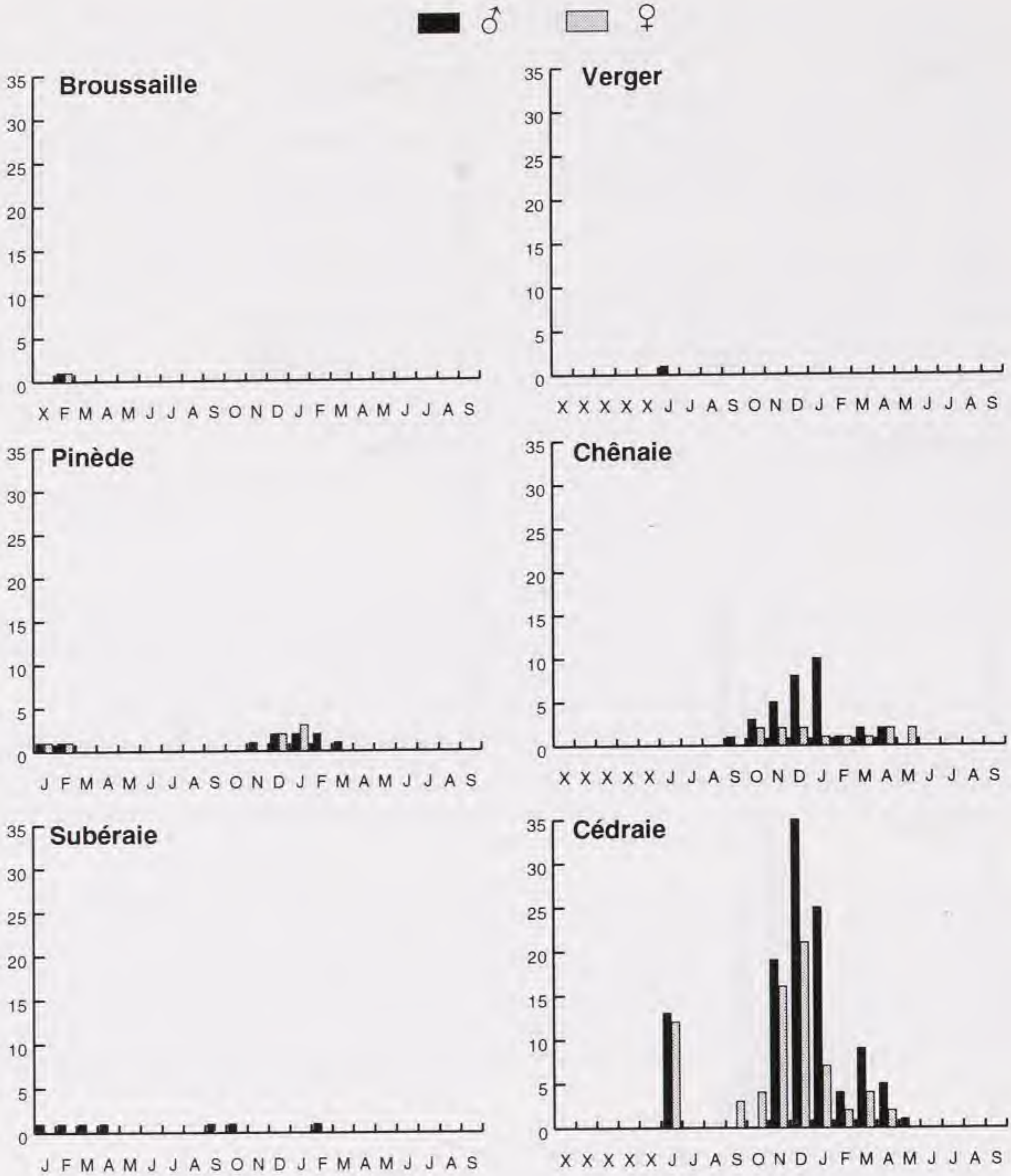


FIG. 7. — Abondance et activité relatives mensuelles de *Phalloiulus distinctus* dans les stations étudiées (x = période non échantillonnée).
FIG. 7. — Relative abundance and activity of Phalloiulus distinctus *in the study sites (x = no sampling).*

Source : MNHN, Paris

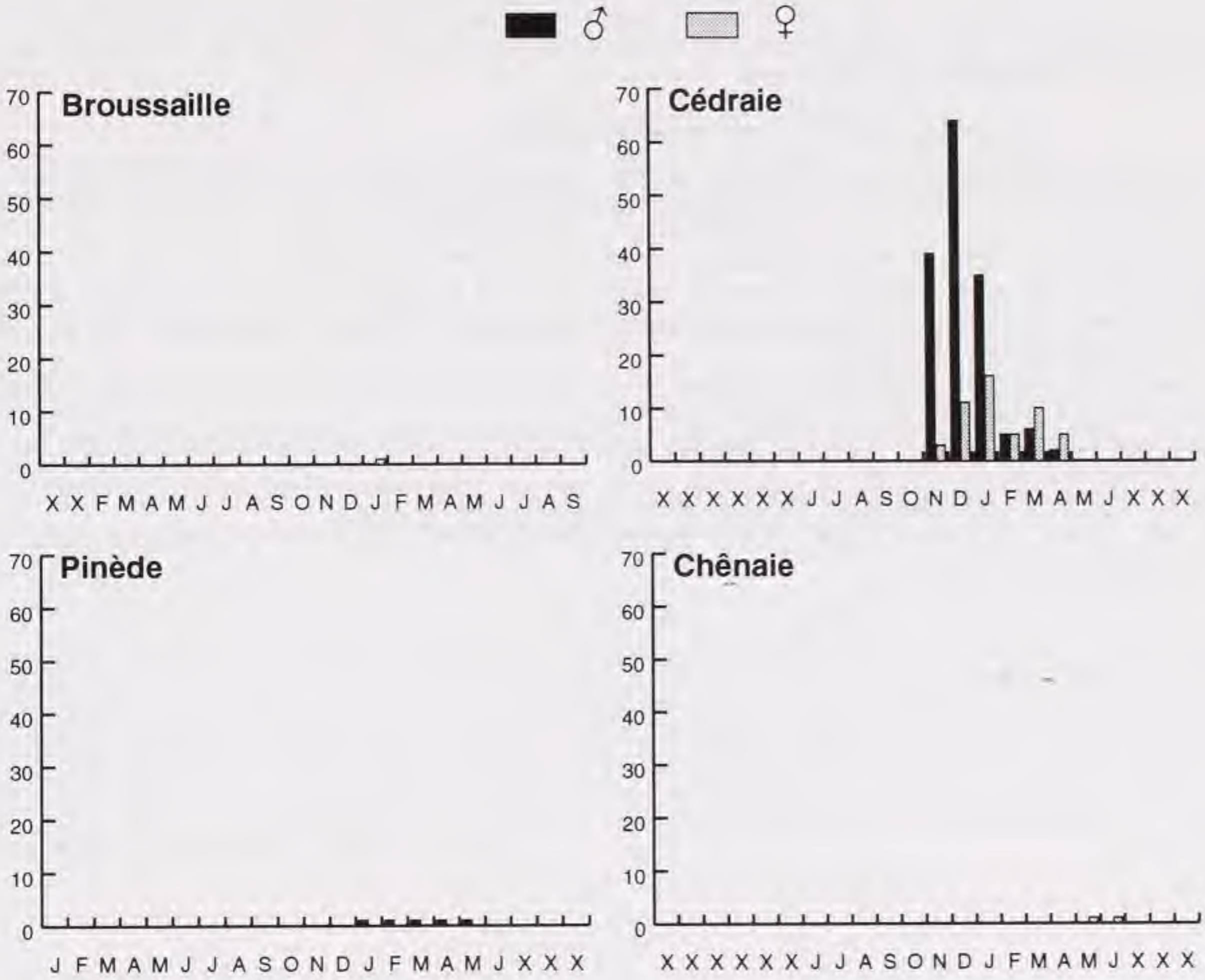


FIG. 8. — Abondance et activité relatives mensuelles de *Archipolydesmus sp.* dans les stations étudiées (x = période non échantillonnée).
FIG. 8. — Relative abundance and activity of Archipolydesmus *sp. in the study sites (x = no sampling).*

La comparaison des listes faunistiques des diverses stations fait apparaître deux points :

1) la répartition plus ou moins uniforme de la plupart des genres et espèces au sein de l'aire concernée par l'étude.

2) l'apparente diversité des habitats dans lesquels une même espèce peut être représentée.

Les populations les plus abondantes montrent une période d'activité pendant l'automne, l'hiver et le printemps ; les mâles sont plus actifs en surface en hiver et les femelles au printemps, les conditions climatiques qui règnent durant l'été rendant difficiles l'accès aux individus installés temporairement dans des sites refuges. L'altitude, associée à l'importance relative de l'humidité, semble représenter un facteur écologique fondamental dans la répartition des espèces de la région étudiée. Au-delà de cette première approche consacrée aux chilopodes et aux diplopodes, d'autres études sont envisagées pour déterminer la nature et l'importance des divers facteurs expliquant l'organisation et les variations de leurs peuplements.

Source : MNHN, Paris

REMERCIEMENTS

Je tiens à remercier vivement le Dr. R. BOSMANS pour son aide dans la récolte du matériel et ses conseils précieux. Je remercie également le Dr. A. SERRA pour la vérification de l'identification des chilopodes et M. J.-P. MAURIÈS pour la vérification de l'identification des diplopodes.

RÉFÉRENCES

BRANDT, C.,1840. — Rapport sur les Oniscides et les Myriapodes dans la régence d'Alger. *Revue Soc. cuviérienne Paris*, **3**.

BRÖLEMANN, H. W., 1897. — Iulides d'Algérie. *Ann. Sc. nat.* , sér . 8, Zool., **4** : 253-276.

BROLEMANN, H. W., 1921. — Liste des Myriapodes signalés dans le nord de l'Afrique. *Bull. Soc. Sc. nat. Maroc*, **1** : 3-6.

BROLEMANN, H. W., 1925. — Races nouvelles de *Schizophyllum* algériens (Myriapodes Diplopodes). *Bull. Soc. Hist. nat. Afrique du Nord*, **16** : 245-253.

BROLEMANN, H. W., 1930. — Myriapodes du Sahara central recueillis par L. G. Seurat au cours de la mission du Hoggar (février-avril 1928). *Bull. Soc. Hist. nat. Alger*, **1** : 6-8.

BROLEMANN, H. W., 1931. — Myriapodes recueillis par Mr. le Dr. H. Gauthier en Algérie. *Bull. Soc. Hist. nat. de l'Afrique du Nord*, **22** : 121-134.

HALIMI, A., 1980. — Atlas blidéen. *Off. Pub. Univ. Alger* : 1-523.

LUCAS, L., 1846. — Notes sur quelques nouvelles espèces d'insectes (Myriapodes) du Nord de l'Afrique. *Rev. zool. Sci. de Cuvier, Paris*, **9** : 283.

Source : MNHN, Paris

Étude des communautés de myriapodes (Chilopoda et Diplopoda) des forêts prépyrénéennes (Huesca, Espagne)

Antoni SERRA *, *Maria Cristina* VICENTE ** & *Eduardo* MATEOS *

* Departament de Biologia Animal, Facultat de Biologia, Universitat de Barcelona, Avda. Diagonal, 645 E-08028 Barcelona, Espagne
** Departament de Biologia Animal, Biologia Vegetal i Ecologia, Facultat de Ciències, Universitat Autònoma de Barcelona, E-08193 Bellaterra, Barcelona, Espagne

RÉSUMÉ

Ce travail est consacré à l'étude des chilopodes et des diplopodes des milieux forestiers du massif de San Juan de la Peña, qui appartient au système prépyrénéen de la province de Huesca (Nord de l'Espagne). Douze stations ont été étudiées : trois pinèdes, deux sapinières, une hêtraie, une forêt mixte, une chênaie, une forêt de chênes verts, deux zones de broussailles et une prairie pâturée. On a utilisé la méthode des pièges d'interception de type BARBER. Six pièges, distants d'au moins 10 m, ont été installés dans chaque station et relevés chaque semaine, de février 1977 à mars 1978. Les aspects suivants ont été pris en considération : composition taxinomique des peuplements, densité relative et activité des chilopodes et des diplopodes, caractérisation de chaque station en fonction de son peuplement en myriapodes et préférences spécifiques pour les différents habitats.

ABSTRACT

Centipede and millipede population study in prepyrenean forests (Huesca, Spain).

This work is devoted to the study of the centipedes and millipedes living in the forest habitats of the San Juan de la Peña mountains, which belongs to the pre-Pyrenean system of the Huesca province (North of Spain). Twelve plots were studied, corresponding to three pine groves, two fir woods, a beechwood, a mixed forest, an oak grove, a holm-oak wood, two brushwoods and a pasture land. The sampling was performed by means of pitfall traps. Six traps, at least 10 m apart, were placed in each plot. The trapping was done weekly from February 1977 to March 1978. The following aspects were investigated : taxonomic composition of the myriapod populations, relative densities of active Chilopoda and Diplopoda during the study period, characterization of each plot on the basis of its myriapod population and specific preferences for the different habitats studied.

INTRODUCTION

Dans ce travail est exposée l'étude réalisée sur un grand échantillonnage de myriapodes (chilopodes et diplopodes) récoltés par des méthodes indirectes sur différents biotopes du Massif de San Juan de la Peña, qui est situé dans la zone prépyrénéenne de la province de Huesca (Espagne).

SERRA, A., VICENTE, M. C. & MATEOS, E., 1996. — Étude des communautés de myriapodes (Chilopoda et Diplopoda) des forêts prépyrénéennes (Huesca, Espagne). *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 187-204. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

Le programme de piégeage a été structuré et exécuté par le Dr. César PEDROCHI-RENAULT de l'Instituto Pirenaico de Ecología de Jaca. 52059 exemplaires de différents groupes d'arthropodes ont été capturés. Le groupe des arachnides est, en nombre, le mieux représenté, tandis que celui des chilopodes présente le plus faible effectif de tout l'ensemble (PEDROCCHI-RENAULT, 1985).

SITE D'ÉTUDE

Le massif de San Juan de la Peña fait partie des Chaînes Prépyrénéennes méridionales ; il se trouve situé dans la province de Huesca, au sud-est de Jacà. Il est essentiellement constitué, du point de vue géologique, de conglomérats deltaïques qui reposent sur les marges de la Dépression Moyenne, et atteint, à son point culminant, le pic de San Salvador, l'altitude de 1546 m. Le climat de la zone est de type subméditerranéen continental, les zones basale et périphérique du massif se trouvant dans la subrégion phytoclimatique IV-VI (ALLUÉ, 1964). L'examen des diagrammes climatiques correspondant aux différentes stations du contour du massif de San Juan de la Peña permet de noter les constantes suivantes (PEDROCCHI-RENAULT, 1985) :

- Les précipitations annuelles oscillent entre 700 et 900 mm, avec un maximum printanier en mai (près de 100 mm) et un minimum en juillet (près de 35 mm). La période sèche est peu intense et de courte durée (mois de juillet seulement).
- La température annuelle moyenne oscille autour de 10°C.
- La moyenne des températures minimales du mois le plus froid (janvier ou décembre) oscille entre -1°C et -2°C, avec des minimales absolues de -13°C.
- La moyenne des températures maximales du mois le plus chaud (juillet ou août) oscille entre 26°C et 28°C, avec des maximales absolues qui atteignent 36°C.
- Dans presque toutes les stations, la période des gelées sûres s'étend de décembre à mars; celle des gelées probables est en avril, octobre et novembre. Les mois de mai à septembre peuvent être considérés comme en dehors des périodes de gélées.
- Dans le centre du massif, à une altitude de 1200 m, on observe une modification importante des conditions climatiques. La période sèche estivale disparaît et le mois de mai présente un caractère perhumide, avec des précipitations supérieures à 100 mm. Les températures maximales d'été ne sont pas si élevées que dans la zone basale et la période des gelées probables se prolongue jusqu'en mai. Des telles caractéristiques permettent d'inclure le massif dans la subrégion phytoclimatique VI, qui est définie par l'absence de périodes sèches et par une longue saison froide, avec une température moyenne du mois le plus froid inférieure à 6°C.

LES STATIONS D'ÉTUDE

Le programme de piégeage a été réalisé sur un total de douze stations situées, à l'exception de la chênaie à *Quercus faginea*, sur le massif de San Juan de la Peña.

Hêtraie

Altitude : 1290 m ; Orientation : N-NE ; Pente : 33°. Sol très profond, riche en carbonates, couvert par une épaisse couche de litière qui rend difficile le développement de la strate muscinale. La strate herbacée est très pauvre et discontinue. La strate arbustive est un peu dense, formée par des buis et quelques houx. Quelques sapins et pins sylvestres accompagnent les hêtres dominants.

Forêt mixte

Altitude : 1105 m ; Orientation : N-NW ; Pente : 20°. Le sol est une rendzine très humifère, avec un horizon organique atteignant 20 cm d'épaisseur. La couche de litière ne permet pas le développement de la couche muscinale. La strate herbacée est dominée par *Hedera helix* qui forme un tapis et même, çà et là, des masses de végétation. La strate arbustive est assez importante en abondance et diversité spécifiques. La strate arborée, avec un recouvrement de 100%, comprend les essences *Tilia platyphyllos, Fraxinus excelsior, Ulmus montana, Fagus sylvatica* et *Abies alba.*

Pinède basse

Altitude : 962 m ; Orientation : N-NE ; Pente : 17°. Sol profond de terre brune, maintenu sur un terrain caillouteux et couvert par une strate muscinale continue. Le buis, bien développé et dense, constitue l'espèce arbustive dominante, avec aussi *Clematis vitalba* et quelques jeunes sapins. *Pinus sylvestris* forme une voûte arborée presque continue.

Pinède moyenne

Altitude : 1120 m ; Orientation : NE ; Pente : 32°. Sol brun, calcaire, profond et couvert d'un strate muscinale dense et abondante. La couche herbacée est abondante si on la compare avec celle d'autres milieux forestiers. La strate

Source : MNHN, Paris

arbustive, avec un épais manteau de buis, contient aussi quelques exemplaires de *Juniperus communis* et de hêtres. La forêt est constituée de *Pinus sylvestris* assez mûrs, très fréquents sur le massif.

Pinède haute

Altitude : 1390 m ; Orientation : W ; Pente : 12°. Sol profond avec des carbonates, couvert de feuilles de hêtre. Les strates muscinale et herbacée sont pauvres. Le niveau arbustif est peu dense et il est dominé par *Buxus sempervirens* et *Ilex aquifolium*. La forêt, éclaircie par la coupe de *Pinus sylvestris*, comprend des hêtres et des sapins.

Sapinière basse

Altitude : 1035 m ; Orientation : N ; Pente : 29°. Sol acide superficiellement, très riche en matière organique, se mélangeant en profondeur avec des cailloux et de l'argile. La strate arbustive est composé par des buis et des hêtres jeunes. La strate arborée se compose de sapins, à 100%, sans aucune autre espèce d'arbre.

Sapinière haute

Altitude : 1415 m ; Orientation : N-NW ; Pente : 25°. Sur la roche-mère, constituée de conglomérats, le sol est profond, riche en humus et de pH acide. Strate muscinale abondante, avec un recouvrement de 50%. Les strates herbacée et arbustive sont très pauvres. La strate arborée est typique d'une forêt en régénération, avec abondance de *Abies alba* jeunes mais peu vigoureux ou mourants, avec beaucoup de bois mort au sol (exemplaires morts et restes de coupe). De rares *Pinus sylvestris* s'intercalent entre les sapins.

Chênaie d'yeuses

Altitude : 940 m ; Orientation : S-SE ; Pente : 27°. Sol de type xérorendzine, peu profond et riche en carbonate de calcium. Même si actuellement la pression humaine est nulle, jusqu'aux années 1940, le pâturage et la coupe des arbres ont diminué la taille de la chênaie qui se réduit actuellement à quelques massifs d'yeuses (chêne vert). En sous-bois, l'absence de lumière ne permet pas l'installation d'autres espèces, et une épaisse couche de feuilles (10 à 15 cm) s'est accumulée. Autour de ces massifs apparaît une bordure arbustive fondamentalement constituée de *Buxus sempervirens* et *Juniperus*. Dans les espaces ouverts apparaissent des plantes qui résistent à des sècheresses prolongées et à des oscillations thermiques importantes, telles que *Thymus vulgaris, Festuca greca indigesta* et quelques *Sedum*. Cette station est la plus méditerranéenne du massif.

Chênaie à Quercus faginea

Altitude : 775 m ; Orientation : N-NW ; Pente : 10°. C'est la seule station qui n'est pas située sur le massif de San Juan de la Peña, mais sur un de ses chaînons. C'est une forêt de régénération de *Quercus faginea* avec une végétation caractéristique du type subméditerranéen montagnard, où l'action du pâturage a été très intense dans le passé. Le sol est une terre brune calcaire, en bon état de conservation.

Fruticée à Echinospartum horridum

Altitude : 1272 m ; Orientation : S-SE ; Pente : 14°. Cette station est établie sur une zone qui a brûlé en 1919 et qui a été repeuplée avec *Pinus sylvestris* en 1965. Après l'incendie, l'érosion a laissé un sol squelettique sur le conglomérat qui affleure souvent. Les aptitudes colonisatrices de la fruticée à *Echinospartum horridum* lui ont permis d'occuper ces aires altérées par le feu, avec le maintien de la communauté antérieure à l'incendie. Les pins, peu vigoureux et ne dépassant pas un mètre de haut, souffrent actuellement de la sécheresse et aussi des attaques de chenilles processionnaires.

Fruticée à Genista scorpius

Altitude : 840 m ; Orientation : S ; Pente : 33°. Cette station est située dans une aire très perturbée par l'homme ; l'abandon du pâturage a été la cause probable de l'invasion de *Genista scorpius*, espèce qui domine actuellement. Le sol, arasé, contient peu de matière organique en surface où affleure souvent la structure argileuse de l'horizon minéral. Outre les genêts, la végétation, caractéristique des zones arides à contrastes thermiques, est composée principalement de *Thymus, Lavandula et Festuca* gr. *indigesta* .

Pâturage

Altitude : 1130 m ; Orientation : N-NE et N-W ; Pente : 10°. Il s'agit de prairies qui ont appartenu à la forêt et dont l'équilibre dépend uniquement de la pression du pâturage ; elles ont été colonisées rapidement par la végétation marginale forestière ou par la fruticéee. Le sol est profond (60 à 100 cm), de terre brune et avec une notable quantité de matière organique en surface. La végétation est toujours herbacée, avec en général des graminées. La zone choisie pour l'échantillonnage a perdu son équilibre à la suite du manque de pâturage. Actuellement, la fruticée à *Echinospartum horridum* s'accroît chaque année, alors qu'apparaissent de jeunes *Pinus sylvestris*.

Source : MNHN, Paris

MATÉRIEL ET MÉTHODES

Le matériel étudié a été collecté à l'aide de pièges de type BARBER de 57 mm de diamètre à l'ouverture ; une solution saturée de chlorure de sodium dans l'eau avec un peu de détergent incolore a été utilisée comme liquide de conservation. Dans chacune des douze stations d'échantillonage, six pièges ont été installés à plus de dix mètres de distance les uns des autres. Le nombre de pièges a été déterminé par un échantillonnage fait avant selon les critères de LAMOTTE *et al.* (1969). Le matériel capturé était récupéré chaque semaine, si les conditions climatiques le permettaient. Le piégeage a été réalisé pendant la période de temps s'étendant de février 1977 à mars 1978.

L'échantillon global de myriapodes est composé de 3760 exemplaires correspondant à 3670 diplopodes et 90 chilopodes. L'ensemble de ces deux groupes représente à peu près 7,5% du total des arthropodes récoltés (52059 exemplaires).

On ne veut pas clore ce paragraphe sans rappeler que l'interprétation des données obtenues avec cette méthode de capture par piège est d'une fiabilité limitée et qu'elle concerne essentiellement les taux d'activité des individus composants une fraction des populations, il faut donc en tenir compte au moment des conclusions (ADIS, 1979; ASCASO, 1984).

REMARQUES FAUNISTIQUES

Le nombre d'espèces de diplopodes répertoriées dans l'ensemble des douze biotopes est de 17. Une dizaine d'entre elles sont pyrénéennes : *Hirudisoma pyrenaeum* Ribaut, 1908 - *Marquetiella lunatum* (Ribaut, 1920) - *Archipolydesmus osellai* Ceuca, 1968 - *Polydesmus racovitzai* Brölemann, 1910 - *Blaniulus dollfusi* Brölemann, 1894 - *Haplopodoiulus spathifer* (Brölemann, 1897) - *Leptoiulus umbratilis* Ribaut, 1905 - *Ommatoiulus robustus* Ceuca, 1974 - *Loboglomeris haasi* Attems,1927 et *Protoglomeris vasconica* (Brölemann, 1897). Le reste des espèces, *Polydesmus coriaceus coriaceus* Porat, 1879, *Cylindroiulus caeruleocinctus* (Wood, 1864), *Ommatoiulus sabulosus* (Linné, 1758), *Tachypodoiulus niger* (Leach, 1815) (= *T. albipes*), *Glomeris hexasticha intermedia* Latzel, 1884 et *Glomeris marginata* (Villers, 1789), sont des espèces de distribution européenne plus ou moins large. Avec ces espèces, trois exemplaires de *Ceratosphys* sp. ont aussi été trouvés mais ils n'ont pas pu être identifiés spécifiquement car il s'agissait d'une femelle et de deux mâles immatures.

A noter que les espèces *H. pyrenaeum, M. lunatum, P. racovitzai* et *L. umbratilis* ont été trouvées pour la première fois dans la Péninsule Ibérique. D'autre part, *A. osellai* est retrouvée pour la première fois depuis sa description originale. Tous ces faits mettent en évidence qu'il reste encore beaucoup de données faunistiques à découvrir sur le versant sud des Pyrénées, même si cette zone est une des mieux connues de la Péninsule Ibérique (MAURIÈS, 1975).

En ce qui concerne les chilopodes (cf. BROLEMANN, 1930 ; EASON, 1964), on remarque que les individus appartenant aux 11 espèces identifiées au cours du piégeage sont beaucoup moins nombreux que pour les diplopodes. Deux des espèces, *Strigamia acuminata* (Leach, 1814) et *Lithobius forficatus* (Linné, 1758) se caractérisent par une répartition holarctique ; cinq autres espèces, *Lithobius borealis* Meinert, 1872, *Lithobius calcaratus* C. Koch, 1844, *Lithobius duboscqui* Brölemann, 1896 (= *L. microps*), *Lithobius piceus* L. Koch, 1862 et *Lithobius tricuspis* Meinert, 1872 présentent différents types de répartition en Europe ; les quatre autres présentent d'autres types de distribution géographique : *Lithobius castaneus* Newport, 1844 est une espèce circumméditerranéenne ; *Lithobius pilicornis* Newport, 1844 est un élément atlantique ; *Lithobius variegatus rubriceps* (Newport, 1845) se trouve en Irlande, Grande-Bretagne, Bretagne et dans la Péninsule Ibérique (EASON & SERRA, 1986) alors que *Nesoporogaster hispanica* Matic & Darabantu, 1969 se trouve dans les Pyrénées espagnoles.

COMPOSITION ET STRUCTURE DES PEUPLEMENTS

Les Figs 1 et 2 représentent les abondances relatives des populations d'espèces de diplopodes et de chilopodes dans l'ensemble des stations. Parmi les diplopodes, l'abondance de *Glomeris marginata* est remarquable, suivie par *Cylindroiulus caeruleocinctus*, *Marquetiella lunatum* et *Glomeris hexasticha intermedia*, qui représentent plus de 10% du total. En ce qui

Source : MNHN, Paris

concerne les chilopodes, *Lithobius borealis* et *Lithobius variegatus rubriceps* ressortent du lot par leur abondance par rapport aux autres espèces représentées.

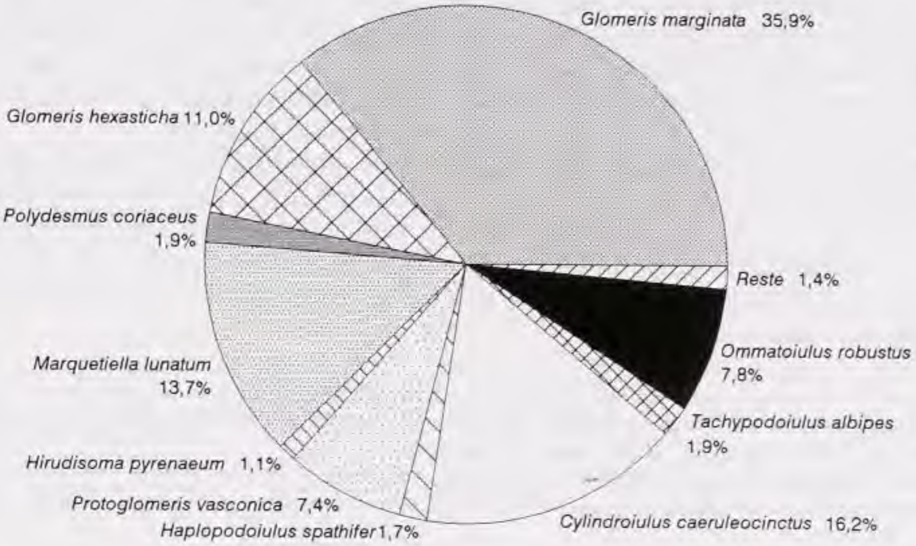


FIG. 1. — Abondance relative des différentes espèces de diplopodes capturées.
FIG. 1. — Relative abundance of the different species of millipedes in the pitfall traps.

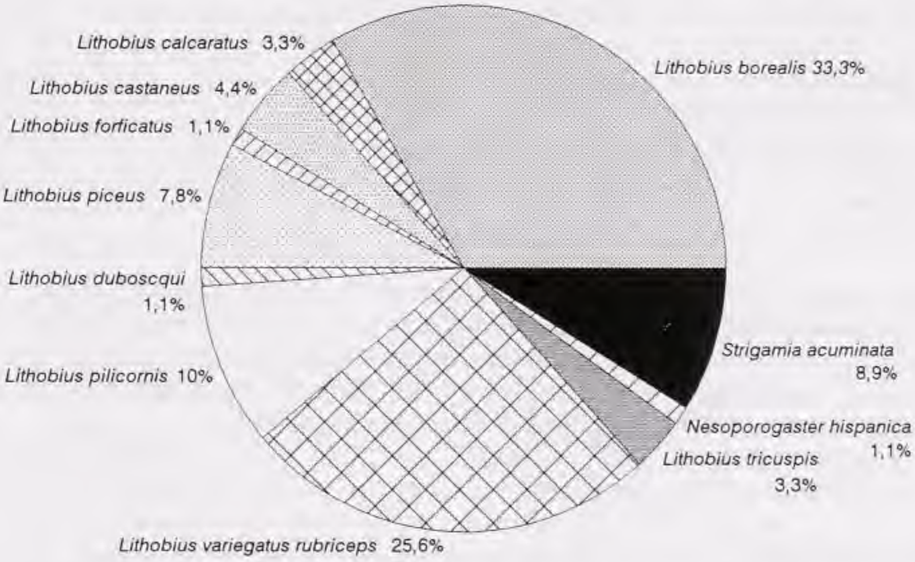


FIG. 2. —Abondance relative des différentes espèces de chilopodes capturées.
FIG. 2. — Relative abundance of the different species of centipedes in the pitfall traps.

Source : MNHN, Paris

Si l'on analyse les données du Tableau 1, on observe que, même si le nombre d'espèces est moindre (et plus marqué pour le nombre d'individus), les valeurs de richesse spécifique, équitabilité et dominance du total des diplopodes sont semblables à celles obtenues pour le total des chilopodes. Le trop petit nombre d'exemplaires de ces derniers ne nous a pas permis d'aborder leur étude précise dans chacune des stations. En revanche, les diplopodes, plus abondants, permettent de réaliser un étude particulière de chaque zone de piégeage. L'ensemble des écosystèmes forestiers, hêtraie, forêt mixte, pinèdes et sapinières, présentent des valeurs d'indice de diversité très proches (de 2,44 à 2,14) et très supérieures aux valeurs des autres stations ; parallèlement les valeurs de dominance d'une ou deux espèces sont relativement faibles et sensiblement inférieures à celles des zones non forestières ou altérées.

Les incendies, l'exploitation du bois et le pâturage constituent des impacts sur une série de stations du massif de San Juan de la Peña qui ont conduit à des altérations notables des associations végétales originales. Même si elles ont actuellement cessé, les perturbations provoquées sur les communautés d'arthropodes continuent à se manifester. Ce que semblent prouver les faibles indices de diversité (de 1,41 à 1,08) et les hautes valeurs de la dominance au sein des populations des diplopodes.

TABLEAU 1. — Nombre d'espèces présentes (N. sp.), indice de diversité de Shannon (H), diversité maximum (Hmax), équitabilité (E), dominance par une [D(i)] ou deux [D(i, j)] populations pour le total des diplopodes, le total des chilopodes et pour les diplopodes de chacune des stations.

TABLE 1. — Specific richness (N. sp.), Shannon diversity index (H), max. diversity (Hmax), equitability (E), dominance by one species [D(i)] or two specific populations [D(i, j)] for the whole Diplopoda, the whole Chilopoda, and the Diplopoda of each site.

	N. sp.	H	Hmax	E	D(i)	D(i, j)
Diplopodes : Total	17	2,77	4,09	67,81	35,88	52,11
Hêtraie	11	2,44	3,46	70,65	32,88	65,09
Forêt mixte	10	2,36	3,32	71,06	36,96	65,76
Pinède basse	13	2,36	3,70	63,83	47,25	67,25
Pinède moyenne	9	2,14	3,17	67,67	43,73	73,48
Pinède haute	7	2,22	2,81	78,99	37,86	67,14
Sapinière basse	10	2,23	3,32	67,05	35,31	59,60
Sapinière haute	6	2,25	2,58	86,97	44,90	60,20
Chênaie d'yeuses	5	1,08	2,32	46,59	61,15	98,43
Chênaie à *Quercus faginea*	11	1,32	3,46	38,29	74,64	90,94
Fruticée à *E. horridum*	8	1,32	3,00	44,17	74,58	87,43
Fruticée à *Genista scorpius*	3	1,17	1,58	74,10	61,67	95,00
Pâturage	11	1,41	3,46	40,65	73,56	86,59
Chilopodes : Total	11	2,70	3,46	78,15	33,33	58,89

La Figure 3 montre le profil d'activité-densité de l'ensemble des chilopodes capturés sur le massif. En général, le nombre d'exemplaires capturés par piège et par jour est très faible, ce qui peut être du aux basses densités de population des chilopodes, surtout si on la compare avec les consommateurs primaires que sont les diplopodes. Les résultats obtenus avec la méthode utilisant des pièges de type BARBER dans d'autres écosystèmes montrent également un faible effectif de chilopodes (ASCASO, 1986 ; SERRA & ASCASO, 1990). Une autre cause probable de ce phénomène peut être que les différentes espèces de chilopodes présentent une mobilité de surface assez limitée ; ce dernier facteur pourrait avoir comme conséquence que la méthode de capture soit peu appropriée pour l'évaluation qualitative et quantitative de leurs populations.

Le principal facteur climatique qui semble avoir influencé le taux de capture des chilopodes est la température. En décembre et janvier, le nombre d'exemplaires capturés est minimum ou nul, ceci correspond aux mois où l'on enregistre les températures minimales plus basses de l'année. Pendant les mois les plus chauds, fin du printemps et été, le nombre d'individus

Source : MNHN, Paris

interceptés par les pièges augmente régulièrement jusqu'à atteindre un maximum au mois de septembre. Toutefois, en mars 1978, on enregistre aussi des valeurs élevées. En tout cas, l'hétérogénéité des taux de capture associée à la possibilité de variations microclimatiques dans les diverses stations rend l'interprétation des résultats particulièrement délicate.

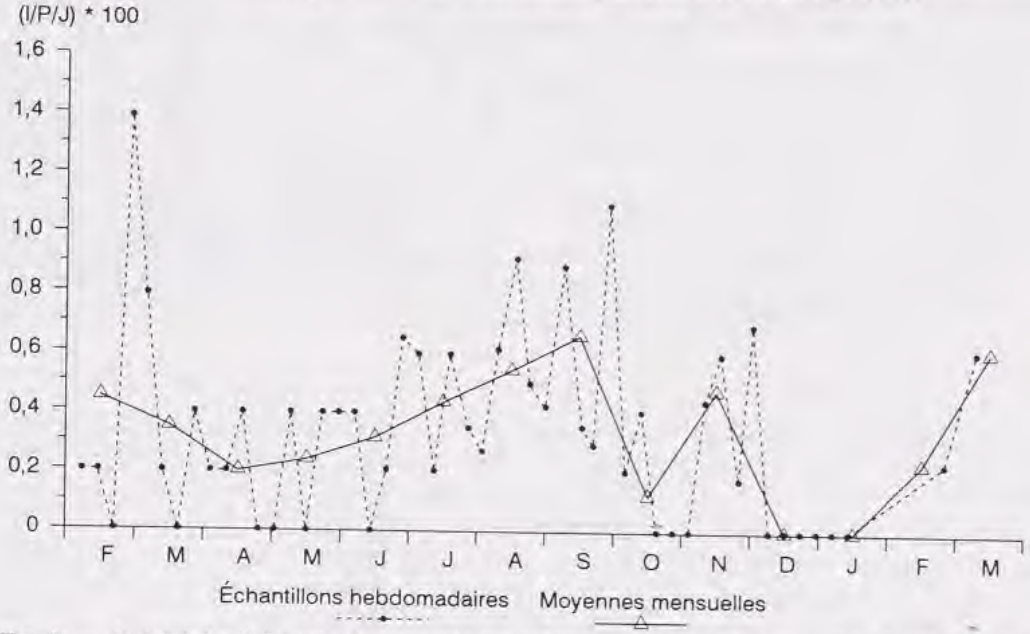


FIG. 3. — Activité-densité (individus capturés par piège et par jour) pour l'ensemble des chilopodes.
FIG. 3. — Activity-density (individuals per pitfall trap per day) for the whole Chilopoda.

ÉTUDE DES PEUPLEMENTS DE DIPLOPODES

Le nombre important de diplopodes capturés nous a permis de réaliser une étude de la composition de leurs populations pour chacune des stations prospectées. Sur les Figures 4 à 27 sont représentés d'un côté les valeurs moyennes annuelles, avec leur déviation standard, des exemplaires de chaque espèce, capturés par piège et par jour [(I/P/J)*100] et de l'autre côté le total des individus capturés par piège et par jour des différentes espèces pour chaque mois pendant la période d'échantillonnage. La Figure 28 correspond à une analyse factorielle de correspondances où les points "espèce" et les points "biotope" sont représentés simultanément. Les abréviations utilisées sur les figures sont détaillées comme suit:

GHE	*Glomeris hexasticha intermedia*
GMA	*Glomeris marginata*
LHA	*Loboglomeris haasi*
PVA	*Protoglomeris vasconica*
AOS	*Archipolydesmus osellai*
PCO	*Polydesmus coriaceus coriaceus*
PRA	*Polydesmus racovitzai*
CCA	*Cylindroiulus caeruleocinctus*
HSP	*Haplopodoiulus spathifer*
LUM	*Leptoiulus umbratilis*
ORO	*Ommatoiulus robustus*
OSA	*Ommatoiulus sabulosus*
TAL	*Tachypodoiulus niger (=albipes)*
BDO	*Blaniulus dollfusi*
CSP	*Ceratosphys* sp.
HPY	*Hirudisoma pyrenaeum*
MLU	*Marquetiella lunatum*

PAT	Pâturage
CHY	Chênaie d'yeuses
FRG	Fruticée à *Genista scorpius*
CHQ	Chênaie à *Quercus faginea*
PIB	Pinède basse
PIM	Pinède moyenne
PIH	Pinède haute
SAB	Sapinière basse
SAH	Sapinière haute
HET	Hêtraie
FMI	Forêt mixte
FRE	Fruticée à *Echinospartum horridum*

Source : MNHN, Paris

Fig.4.- Pâturage

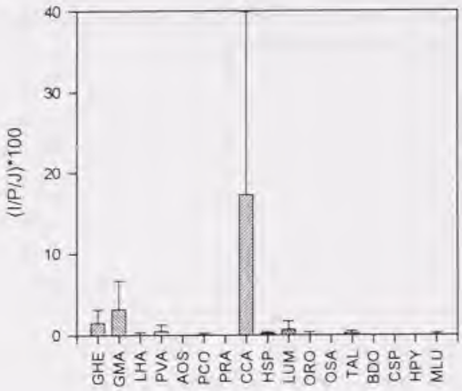


Fig.5.- Pâturage

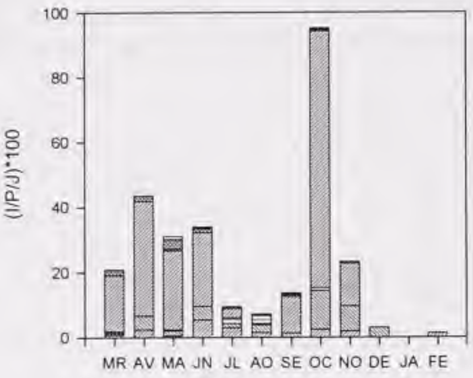


Fig.6.- Fruticée (Gen.)

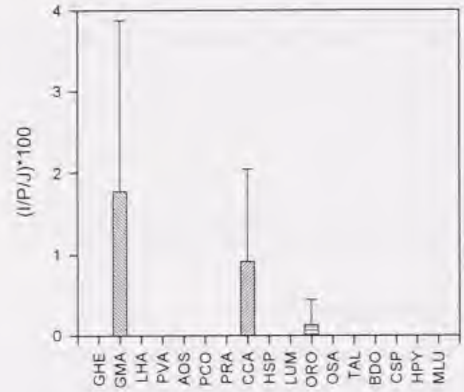


Fig.7.- Fruticée (Gen.)

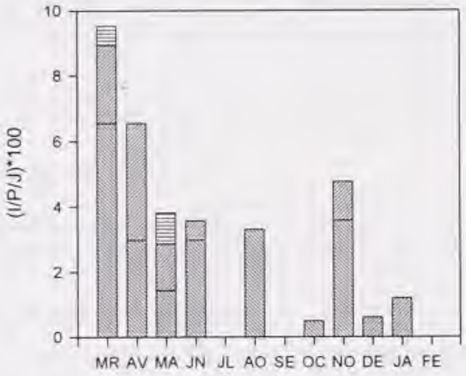


Fig.8.- Chênaie d'yeuses

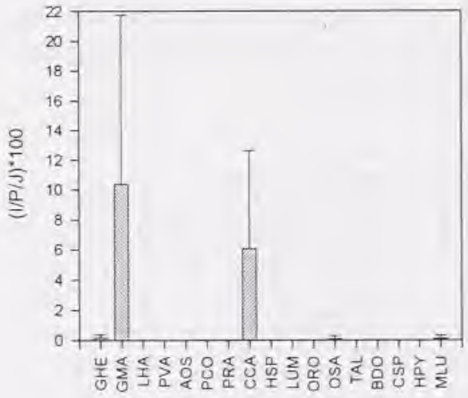
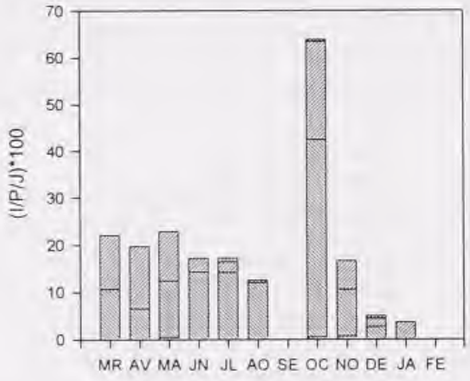


Fig.9.- Chênaie d'yeuses



FIGS. 4-9. — Valeurs moyennes annuelles, avec leur erreur standard, du taux de capture pour chaque espèce (Figs. 4, 6, 8) et taux de capture mensuel des différentes espèces pendant la période de piégeage (Figs. 5, 7, 9) pour les stations Pâturage (4, 5), Fruticée à *Genista* (6, 7) et Chênaie d'yeuses (8, 9). Se reporter au texte pour les abréviations.

FIGS. 4-9. — Annual mean trappability, with standard deviation, for each species (Fig. 4, 6, 8) and monthly trappability for the different species during the trapping period (Fig. 5, 7, 9) respectively for Pasture (4,5), Genista *fruit-tree site (6, 7) and Oak* Q. ilex *(8, 9). See the text for abbreviations.*

Source : MNHN, Paris

Pâturage

Dans cette station sont représentées 11 espèces. *Cylindroiulus caeruleocinctus* est la population la plus abondante, ce qui concorde avec les préférences de cette espèce pour les zones claires. *Glomeris marginata* est la plus fréquente ; elle se rencontre toute l'année sauf en janvier et en février. Le graphique de l'activité annuelle présente deux valeurs maximales, l'une en avril et l'autre en octobre (cette dernière est le maximum annuel). A partir de ce point, il y a une brusque diminution pendant l'hiver avec des valeurs nulles au mois de janvier. L'activité augmente pendant le printemps et diminue remarquablement pendant les mois d'été, coïncidant avec les températures élevées provoquées par l'insolation et la diminution des précipitations.

En ce qui concerne la phénologie des différentes espèces, on observe que *Cylindroiulus caeruleocinctus* présente son activité maximale en avril et en octobre, *Glomeris hexasticha intermedia* au mois de juin et aussi en octobre, *Glomeris marginata* en octobre, *Protoglomeris vasconica* en août et *Leptoiulus umbratilis* en mai. Pour les autres populations, il est impossible de conclure à cause de leurs fréquence et abondance trop faibles (Figs. 4 et 5).

Fruticée à Genista scorpius

Il s'agit de l'écosystème le plus pauvre en nombre d'espèces présentes (3!), et aussi en nombre d'exemplaires capturés, seulement 60. *Glomeris marginata* est le diplopode le plus abondant et *Cylindroiulus caeruleocinctus* le plus fréquent.

L'activité annuelle est irrégulière et caractérisée par l'absence de captures aux mois de juillet, septembre et février. Comme sur la station de l'autre fruticée, la valeur maximale de l'activité est située en mars, le seul mois, avec le mois de mai, où les trois espèces apparaissent simultanément. *Glomeris marginata* s'y trouve régulièrement pendant le printemps, disparaît pendant quelques mois en été et réapparaît en automme. Au contraire, *Cylindroiulus caeruleocinctus* , totalement absent dans les piègeages d'été est présent en automme et au début de l'hiver (Figs. 6 et 7).

Chênaie d'yeuses

On remarque que si le nombre d'espèces présentes est faible (5) sur cette station, le nombre total d'exemplaires est élevé, ce qui est dû surtout à l'abondance de *Glomeris marginata* et à l'importante fréquence de *Cylindroiulus caeruleocinctus.*

L'activité annuelle est caractérisée par des valeurs peu élevées enregistrées à la fin de l'automme et en hiver, plus fortes en mars, quand les températures commencent à augmenter. Ces valeurs se maintiennent de façon similaire jusqu'à en juillet, époque de températures élevées et de sécheresse et, à partir de ces dates, elles diminuent jusqu'à être nulles en septembre. En octobre, avec l'augmentation des pluies et les températures plus douces, on note un fort accroissement de l'activité, c'est à ce moment qu'on observe le maximum annuel.

Cylindroiulus caeruleocinctus présente une population qui est stable au printemps, dont l'activité diminue considérablement en été pour atteindre sa valeur maximale en octobre, comme *Glomeris marginata*. Ce dernier semble mieux supporter la période estivale, car il maintient et même augmente son activité au cours des mois d'été (Figs. 8 et 9).

Chênaie à Quercus faginea

Malgré une remarquable richesse spécifique sur cette station (11 espèces), la majorité des espèces est très peu représentée, car les 3/4 des exemplaires recueillis sont des *Glomeris marginata,* l'espèce de loin la plus abondante, suivie par *Glomeris hexasticha intermedia*. Ces deux espèces sont aussi les plus fréquentes, présentes dans les pièges pendant 9 des 12 mois étudiés.

Sur le graphique représentant les variations annuelles on remarque que, après le maximum annuel de captures du mois d'octobre, l'activité diminue brutalement jusqu'à sa disparition

Source : MNHN, Paris

presque totale fin octobre et au début de l'hiver. L'activité, avec des valeurs plus ou moins fluctuantes, se maintient pendant le printemps et l'été, et diminue de nouveau au cours du mois de septembre (Figs. 10 et 11).

Sapinière haute

On y trouve 6 espèces. La population dominante est *Marquetiella lunatum*, avec 44 individus récoltés sur un total de 98. De plus, *Marquetiella lunatum* est l'espèce la plus fréquente car elle apparaît pendant toute l'année sauf en août et septembre. On observe que l'activité est faible en février et mars, commence à croître en mars jusqu'au début de l'été et diminue rapidement pour atteindre les valeurs minimales de septembre. Ce phénomène est suivie d'une nouvelle augmentation jusqu'en janvier où se situe le maximum annuel. *Marquetiella lunatum* montre son maximum d'activité en automme et en hiver, comme les autres craspédosomatides.

On peut distinguer trois groupes de populations dans cet écosystème :

a) celles dont l'activité maximale est centrée en fin de printemps et en été comme dans le cas de *Glomeris marginata* ;

b) celles dont l'activité présente deux maxima, l'un en été (juillet) et l'autre en automme (octobre) : *Protoglomeris vasconica, Glomeris hexasticha intermedia, Polydesmus coriaceus coriaceus* et *Haplopodoiulus spathifer* ;

c) celles dont le maximum d'activité se situe en automme et en hiver : *Marquetiella lunatum*. On peut penser que ces activités maximales coïncident avec les périodes de reproduction, mais on ne peut toutefois pas négliger certains phénomènes d'attraction qui peuvent se produire avec le type de pièges utilisés (Figs. 12 et 13).

Sapinière basse

Dans cette station de moindre altitude (1035 m) que la précédente (1415 m), on observe une plus grande richesse spécifique, dix populations au total. La plus fréquente est *Glomeris hexasticha intermedia*, car elle est seulement absente en janvier et en février, et la plus abondante est *Glomeris marginata* qui représente presque le tiers du total des exemplaires.

L'activité dans la sapinière basse est minimale pendant le mois de février, augmente progressivement au printemps jusqu'au début de l'été, où se situe le maximum annuel. La diminution des valeurs d'activité-densité pour les mois les plus chauds est beaucoup moins accentuée que pour la sapinière haute, ceci pouvant être dû à l'effet protecteur de l'abondante strate arbustive de la sapinière basse, valeurs que l'on retrouve au début de l'automme. A partir de ce moment les valeurs diminuent rapidement jusqu'à la fin de l'hiver, où seul *Marquetiella lunatum* apparaît. L'augmentation de l'activité en mars est due à deux causes : a) on y trouve 7 populations du peuplement et b) *Glomeris hexasticha intermedia* et *Glomeris marginata* présentent un nombre élevé (qui ne correspond pas aux valeurs maximales) d'exemplaires.

Concernant les populations, on trouve des espèces ayant une activité maximale en été (juillet), telles que *Protoglomeris vasconica* et *Haplopodoiulus spathifer*, d'autres ayant une activité maximale en fin de printemps et en été (juillet), comme *Glomeris marginata*, des espèces à activité maximale en été (juillet) et en automme (octobre), comme *Glomeris hexasticha intermedia* et des espèces à activité maximale en hiver, comme *Marquetiella lunatum* (Figs. 14 et 15).

Hêtraie

La richesse spécifique de la hêtraie est remarquable, avec un total de 11 espèces présentes. *Glomeris marginata* et *Marquetiella lunatum* représentent d'une façon générale les 2/3 du total des exemplaires ; en outre, on observe que *Marquetiella lunatum* est le diplopode le plus abondant et le plus fréquent.

Source : MNHN, Paris

Fig.10.- Chênaie (Que.)

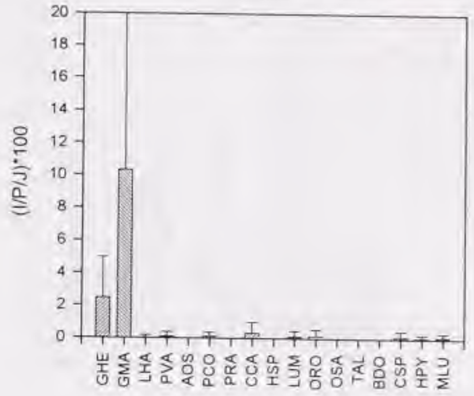


Fig.11.- Chênaie (Que.)

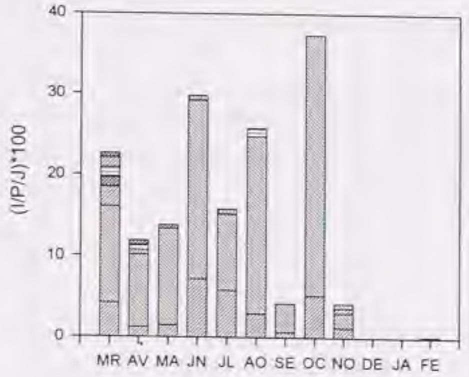


Fig.12.- Sapinière haute

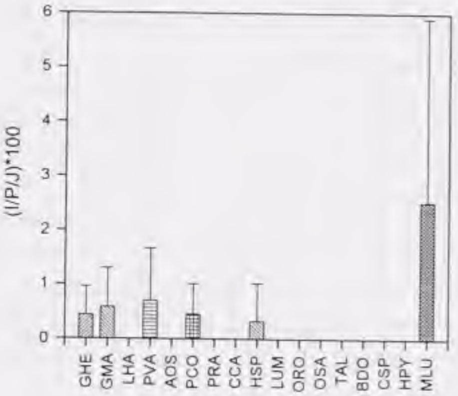


Fig.13.- Sapinière haute

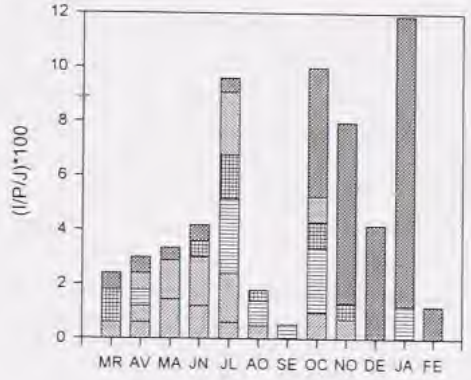


Fig.14.- Sapinière basse

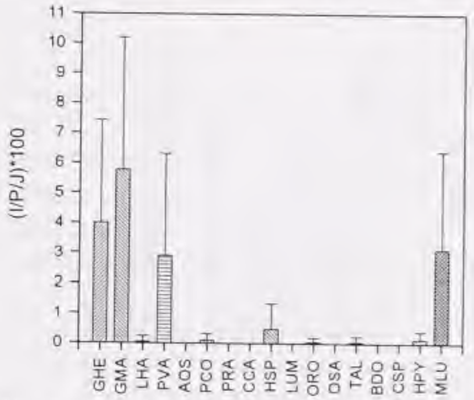
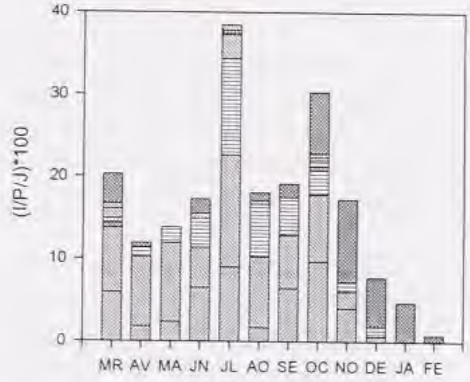


Fig.15.- Sapinière basse



FIGS. 10-15.— Valeurs moyennes annuelles, avec leur erreur standard, du taux de capture pour chaque espèce (Figs. 10, 12, 14) et taux de capture mensuel des différentes espèces pendant la période de piégeage (Figs. 11, 13, 15) pour les stations Chênaie (10, 11), Sapinière haute (12, 13) et Sapinière basse (14, 15). Se reporter au texte pour les abréviations.

FIGS 10-15.— Annual mean trappability, with standard deviation, for each species (Figs 10, 12, 14) and monthly trappability for the different species during the trapping period (Figs 11, 13, 15) respectively for Oak wood (10, 11), High fir-wood (12, 13) and low fir-wood (14, 15). See the text for abbreviations.

Source : MNHN, Paris

Fig.16.- Hêtraie

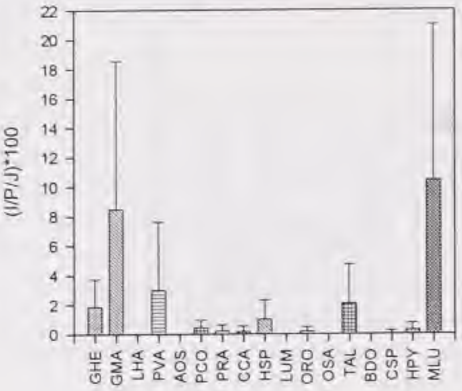


Fig.17.- Hêtraie

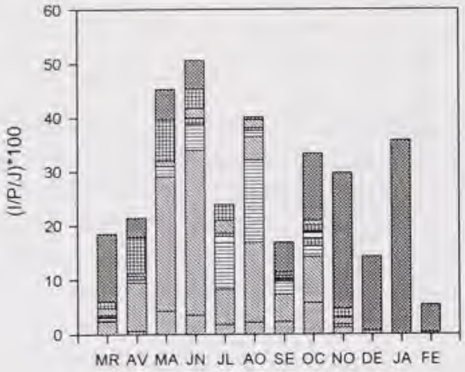


Fig.18.- Pinède haute

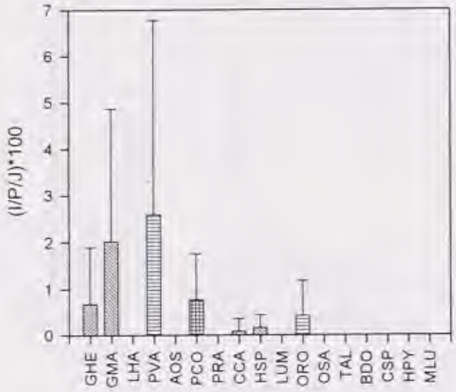


Fig.19.- Pinède haute

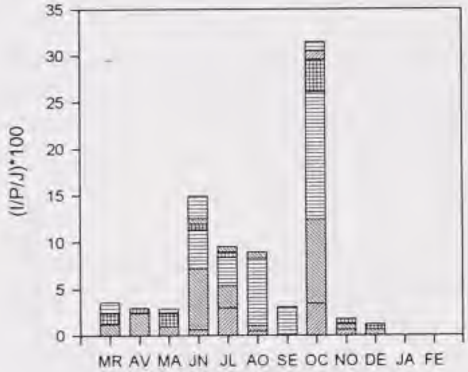


Fig.20.- Pinède moyenne

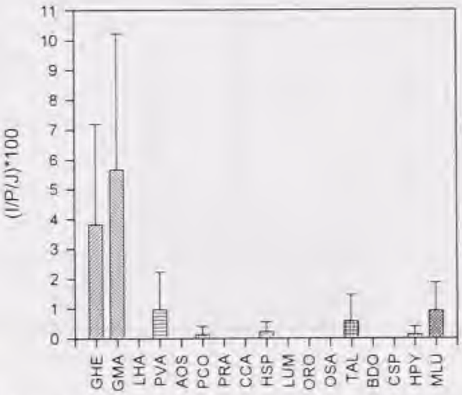
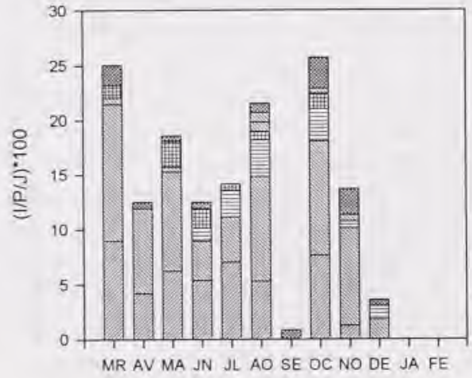


Fig.21.- Pinède moyenne



FIGS. 16-21.— Valeurs moyennes annuelles, avec leur erreur standard, du taux de capture pour chaque espèce (Figs. 16, 18, 20) et taux de capture mensuel des différentes espèces pendant la période de piégeage (Figs. 17, 19, 21) pour les stations Hêtraie (16, 17), Pinède haute (18, 19) et Pinède moyenne (20, 21). Se reporter au texte pour les abréviations.

FIGS 16-21.— Annual mean trappability, with standard deviation, for each species (Figs 16, 18, 20) and monthly trappability for the different species during the trapping period (Figs 17, 19, 21) respectively for Beechwood (16, 17), High pine-wood (18, 19) and medium pine-wood (20, 21). See the text for abbreviations.

Source : MNHN, Paris

L'activité annuelle est caractérisée par l'existence de plusieurs augmentations alternées avec des diminutions. Le maximum annuel de l'activité-densité est atteint en début de l'été, du fait de la présence de *Glomeris marginata*. Pendant quelques mois d'hiver il existe aussi des valeurs élevées dues à la présence de *Marquetiella lunatum*.

On observe que *Glomeris hexasticha* présente deux valeurs maximales, l'une au printemps et l'autre en automme (mai et octobre). *Haplopodoiulus spathifer, Hirudisoma pyrenaeum* et *Protoglomeris vasconica* présentent seulement un maximum en août et au contraire, *Tachypodoiulus niger* (= *T. albipes*) semble être plus actif au cours du printemps et au début de l'été (Figs. 16 et 17).

Pinède haute

Dans cette station, où apparaissent 7 espèces, on remarque l'absence de *Marquetiella lunatum,* malgré l'altitude de la forêt (1390 m) favorable à cette espèce. L'orientation Ouest de cette parcelle et l'absence de sous-bois provoquant un ensoleillement du sol assez intense pourraient expliquer cette absence. L'espèce la plus abondante est *Protoglomeris vasconica* et les plus fréquentes, *Glomeris marginata* et *Polydesmus coriaceus coriaceus*, sont absentes seulement en janvier, février et septembre.

L'activité annuelle présente deux maxima, l'un au mois de juin et l'autre en octobre, ce dernier correspondant au maximum annuel. On observe, dans cet écosystème, un déplacement du pic estival du mois de juillet à juin, l'importante augmentation de l'activité de mai à juin, la diminution qui se poursuit jusqu'en octobre et l'absence totale d'activité en janvier et février (absence de *Marquetiella lunatum* !). Les températures élevées du sol durant les mois d'été, dues à l'absence de sous-bois, la diminution des pluies, peuvent expliquer l'intense activité en juin puis la diminution estivale, tandis que la grande activité d'octobre est la conséquence des températures douces et de l'augmentation des pluies.

En ce qui concerne la phénologie, on trouve des espèces avec des maxima d'activité en fin de printemps-début d'été et en automme, comme *Glomeris marginata*, des espèces avec deux maxima d'activité, l'un en été et l'autre en automme (octobre), comme *Glomeris hexasticha intermedia* et *Protoglomeris vasconica* et finalement on trouve des espèces avec un seul maximum d'activité en fin de printemps-début d'été comme *Ommatoiulus robustus* (Figs. 18 et 19).

Pinède moyenne

Dans cette forêt, 9 espèces ont été capturées, parmi lesquelles *Glomeris marginata* est la plus abondante, car elle représente approximativement la moitié des exemplaires capturés. Elle est aussi la plus fréquente. En second lieu, on observe *Glomeris hexasticha intermedia* qui présente des valeurs d'activité-densité bien inférieures, mais a une abondance moyenne annuelle très supérieure aux autres espèces ; en outre, elle est présente pendant les mêmes mois que *Glomeris marginata* sauf en décembre.

Comme dans la majorité des stations, le mois de septembre est caractérisé par un minimum du nombre de captures suivi d'un notable accroissement en octobre, où sont atteintes les valeurs maximales annuelles. Cependant, on remarque dans cette pinède qu'en fin d'été il y a un accroissement important de l'abondance des diplopodes, qui présente un pic au mois d'août. En hiver, l'activité décroit jusqu'à être nulle en janvier et février ; on remarque l'abondance de *Protoglomeris vasconica* parmi les captures de décembre (Figs. 20 et 21).

Pinède basse

Cette station est celle qui présente la plus grande richesse spécifique parmi toutes les zones étudiées, avec un total de 13 espèces. La plus abondante et aussi la plus fréquente est *Glomeris marginata*.

Source : MNHN, Paris

Fig.22.- Pinède basse

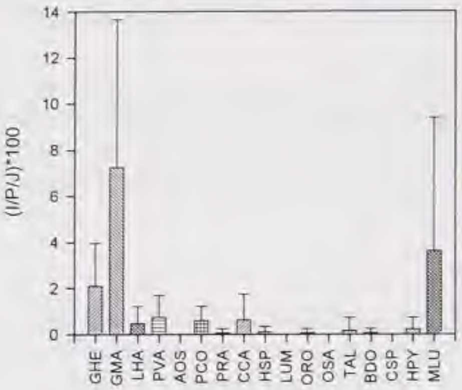


Fig.23.- Pinède basse

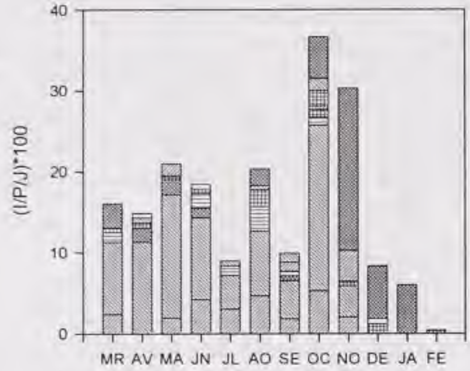


Fig.24.- Forêt mixte

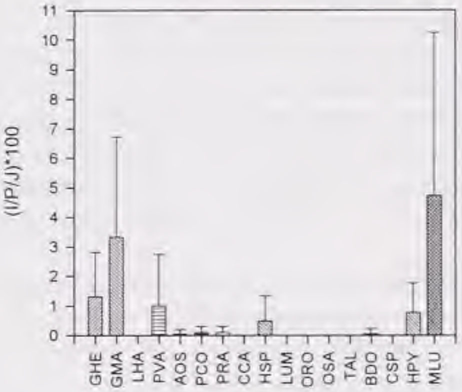


Fig.25.- Forêt mixte

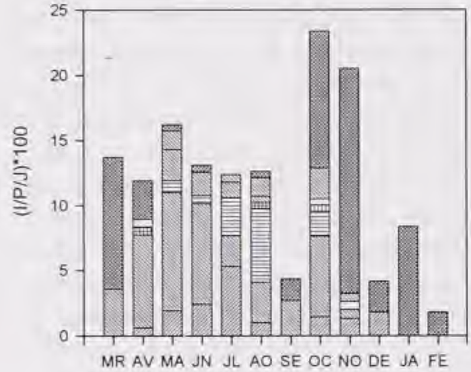


Fig.26.- Fruticée (Ech.)

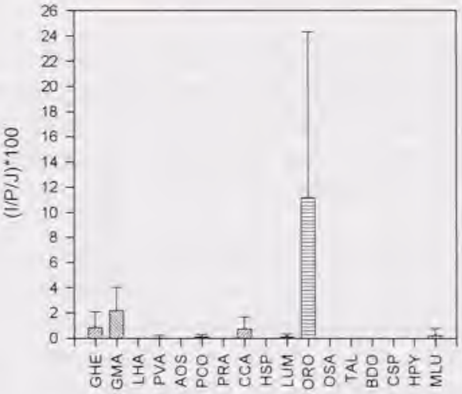
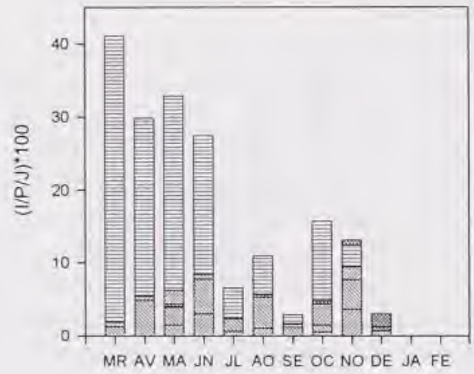


Fig.27.- Fruticée (Ech.)



FIGS. 22-27.— Valeurs moyennes annuelles, avec leur erreur standard, du taux de capture pour chaque espèce (Figs. 22, 24, 26) et taux de capture mensuel des différentes espèces pendant la période de piégeage (Figs. 23, 25, 27) pour les stations Pinède basse (22, 23), Forêt mixte (24, 25) et Fruticée à *Echinospartum* (26, 27). Se reporter au texte pour les abréviations.

FIGS 22-27.— Annual mean trappability, with standard deviation, for each species (Figs 22, 24, 26) and monthly trappability for the different species during the trapping period (Figs 23, 25, 27) respectively for low pine-wood (22, 23), Mixed forest (24, 25) and Echinospartum *fruit-tree site (26, 27). See the text for abbreviations.*

Source : MNHN, Paris

Si l'on observe le profil de l'activité-densité, on constate que la valeur maximale correspond, comme dans les autres pinèdes, au mois d'octobre. Pendant le mois suivant les valeurs enregistrées sont encore notablement élevées, mais à partir de décembre il y a une brusque diminution de l'activité qui atteint son minimum en février. L'espèce la plus active pendant cette période est *Marquetiella lunatum*. Au printemps et en été, les captures sont nombreuses, surtout en août. En revanche en septembre, même si l'activité décroît, on n'atteint jamais les valeurs minimales observées sur les autres stations (Figs. 22 et 23).

Forêt mixte

Aussi bien par son abondance relative que par sa fréquence de capture, l'espèce dominante dans cette forêt est *Marquetiella lunatum*. La deuxième est *Glomeris marginata*, qui présente une fréquence sensiblement moindre. L'activité-densité montre des ressemblances avec les autres pinèdes. En effet, les valeurs maximales se situent en automme et, après une diminution hivernale, il se produit, au printemps, une nouvelle augmentation conduisant à un niveau qui se maintient jusqu'à la fin d'été. Au mois de septembre, comme dans beaucoup d'autres stations, on enregistre une notable diminution de l'activité.

Glomeris hexasticha intermedia possède un maximum en juillet, *Glomeris marginata* présente ses maxima en mai et octobre, *Protoglomeris vasconica* en août, *Haplopodoiulus spathifer* en mai et *Marquetiella lunatum* en octobre et novembre (Figs. 24 et 25).

Fruticée à Echinospartum horridum

Cette station est remarquable par la grande abondance des *Ommatoiulus robustus*. La fréquence maximale est le fait de deux populations, *Ommatoiulus robustus* et *Glomeris marginata*, qui, simultanément, sont absentes en janvier et en février.

Le profil de l'activité-densité montre l'existence de deux maxima ; le premier correspond aux mois de printemps et au début de l'été et le deuxième à l'automme. Curieusement, le maximum de l'activité est atteint en mars à cause de la remarquable abondance de *Ommatoiulus robustus*. Comme en d'autres stations, pendant les mois d'été l'activité décroît notablement et atteint un minimum pendant le mois de septembre (Figs. 26 et 27).

La Figure 28 représente l'analyse factorielle de correspondances réalisée à partir de la matrice des valeurs totales d'individus capturés par piège et par jour des 17 populations de diplopodes dans chacune des douze stations étudiées. Le premier axe, qui explique 39,5% de la variance, sépare la fruticée à *Echinospartum horridum*, qui correspond à une ancienne forêt incendiée comme nous l'avons mentionné antérieurement, du reste des stations. Le second axe, qui interprète 34,2% de la variance, sépare clairement, d'une part, les trois types d'associations végétales, le pâturage, les végétations arbustives de la chênaie d'yeuses et la fruticée à *Genista scorpius* et, d'autre part, les différentes types de forêts. Parmi ces derniers, on sépare légèrement du reste la chênaie à *Quercus faginea* qui présente une végétation typique de l'étage subméditerranéen montagnard altéré par le pâturage ; ces caractéristiques la rapprochent des conditions observées sur les deux associations arbustives.

Chacune de ces communautés végétales est caractérisée par différentes espèces de diplopodes qui montrent des préférences claires pour chacune d'elles. Le pâturage présente comme espèces caractéristiques *Cylindroiulus caeruleocinctus* et *Leptoiulus umbratilis* ; ces deux espèces se trouvent aussi dans les associations végétales de type arbustif. Parmi ces dernières, la chênaie d'yeuses abrite aussi *Ommatoiulus sabulosus*, espèce exclusive de cette station. La fruticée à *Echinospartum horridum* est caractérisée par *Ommatoiulus robustus*, population la plus abondante de la station, comparativement à tous les autres sites. Finalement, ce sont les stations forestières qui hébergent le plus grand nombre d'espèces de diplopodes, en présentant quelques spécificités au niveau de leur abondance relative et de leur fréquence. Il est clair que la

Source : MNHN, Paris

majorité des diplopodes du massif de San Juan de la Peña montre une remarquable préférence pour les milieux forestiers.

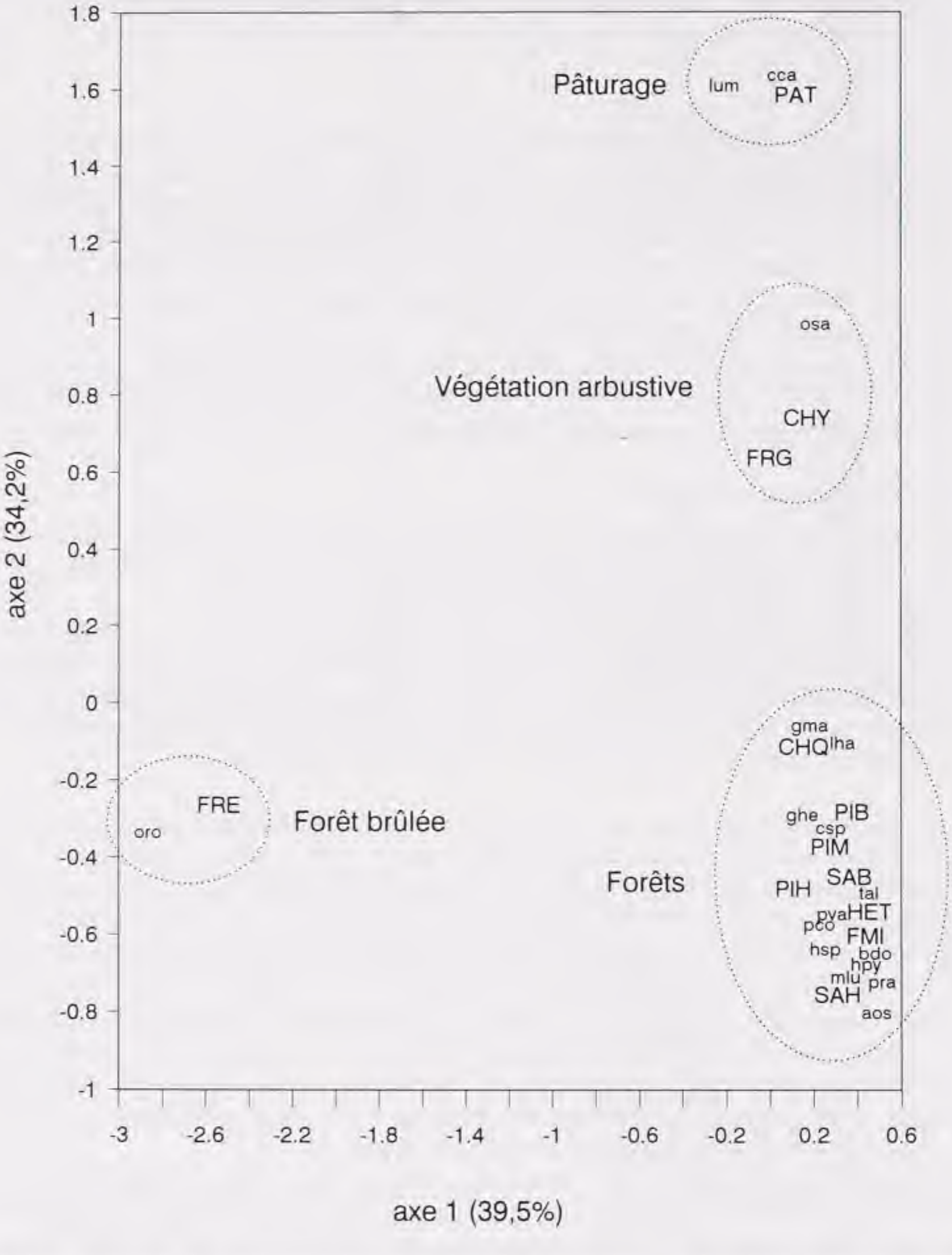


FIG. 28. — Analyse factorielle de correspondances dans laquelle sont représentés les points espèce et les points station.
FIG. 28. — Factorial analysis of correspondences showing species and sites data.

Source : MNHN, Paris

CONCLUSION

De l'analyse des données obtenues avec l'étude des spécimens capturés par les pièges de type BARBER on voit que le nombre de diplopodes est sensiblement plus grand que celui des chilopodes : 1) probablement parce que les chilopodes, prédateurs, sont moins abondants dans les écosystèmes étudiés ; 2) parce que le plus faible nombre de captures semble indiquer que la mobilité de surface des chilopodes est inférieure à celle des diplopodes. Il faut tenir compte en cela du faible nombre de géophilomorphes, propres aux horizons organiques ou minéraux plus profonds, qui ont été capturés.

Les préférences pour des compartiments édaphiques plus ou moins profonds pourraient laisser penser que l'utilisation de pièges d'interception donne des résultats biaisés et sous-estimés des populations de chilopodes. L'étude comparée des résultats obtenus avec l'utilisation simultanée de deux méthodes d'échantillonnage, pièges de type BARBER et biocénomètres ou sondes édaphiques par exemple, dans le même biotope, permettrait de confirmer cette hypothèse et surtout donnerait une estimation d'une part des densités des populations de chaque espèce et d'autre part de la mobilité potentielle de chacune d'elles.

De l'étude des communautés de diplopodes on conclut que les différentes espèces montrent, au moins dans quelques cas, des préférences pour les différents types d'associations végétales présentes à San Juan de la Peña. Les milieux forestiers non altérés, hêtraies, sapinières, pinèdes et forêts mixtes, constituent des écosystèmes où les peuplements de diplopodes montrent une plus grande diversité. Sur un total de 17 espèces de diplopodes représentées dans les captures, 13 ont une nette préférence pour ce type de milieu, étant donné les valeurs élevées d'abondance relative et de fréquence de capture obtenues. L'altération des milieux naturels suite à la coupe de bois, au pâturage ou aux incendies a comme conséquence une diminution notable de la diversité des communautés de diplopodes. L'abondance des populations de beaucoup d'espèces diminue, jusqu'à disparition, tandis que d'autres semblent être favorisées par ces altérations et augmentent remarquablement leur importance numérique. Les valeurs élevées de la dominance que l'on observe, pour une ou deux espèces, sur les stations déstabilisées, illustrent bien ce phénomène. Dans ce sens il faut mentionner *Cylindroiulus caeruleocinctus* et *Leptoiulus umbratilis* qui montrent une nette préférence pour la station de pâturage et, à un degré moindre, pour la fruticée à *Genista scorpius* et la chênaie d'yeuses. *Ommatoiulus sabulosus* est exclusif de la chênaie d'yeuses et *Ommatoiulus robustus* manifeste une affinité remarquable par la fruticée à *Echinospartum horridum*. De plus, il faut tenir compte du fait que l'effet de perturbation du milieu est durable. À l'exception des pâturages qui continuaient à être soumis à cette activité pendant la période de piégeage elle-même, ce facteur déstabilisant avait disparu depuis déjà de nombreuses années dans les stations à fruticées et dans la chênaie d'yeuses.

RÉFÉRENCES

ADIS, J., 1979. — Problems of intercepting arthropod sampling with pitfall traps. *Zool. Anz.*, **202** : 171-185.

ALLUÉ, J. L., 1964. — *Subregiones fitoclimáticas de España. Ministerio de Agricultura.* Madrid, Instituto Forestal de Investigaciones y Experiencias.

ASCASO, C., 1984. — Utilización de trampas de caída en dos comunidades forestales de la región mediterránea: observaciones. *In* : Actas II Congreso Ibérico de Entomología. *Bolm. Soc. Port. Ent.*, **Suppl. 1** : 497-505.

ASCASO, C., 1986. — Estudio cuantitativo de poblaciones a partir de muestreos indirectos: aplicación a comunidades de Artrópodos en dos bosques del Montseny. Tesis Doctoral. Barcelona, Publ. Univ. Autònoma de Barcelona.

BROLEMANN, H. W., 1930. — *Éléments d'une Faune des Myriapodes de France. Chilopodes.* [*Faune Fr.*, **25**] Paris, P. Lechevalier : 1-405.

EASON, E. H., 1964. — *Centipedes of the British Isles.* London, F. Warne & Co Ltd, 294 pp.

EASON, E. H. & SERRA, A., 1986. — On the geographical distribution of *Lithobius variegatus* Leach, 1814, and the identity of *Lithobius rubriceps* Newport, 1845. (Chilopoda, Lithobiomorpha). *Journal nat. Hist.*, **20** : 23-29.

Source : MNHN, Paris

LAMOTTE, M., GILLON, D., GILLON, Y. & RICOU, G., 1969. — L'échantillonnage quantitatif des peuplements d'invertébrés en milieux herbacés. *In : Problèmes d'écologie : l'échantillonnage des peuplements animaux des milieux terrestres.* Paris, Masson : 7-54.

MAURIÈS J. P., 1975. — Diplopodes épigés et cavernicoles des Pyrénées espagnoles et des Monts Cantabriques. VIII. Liste récapitulative, additions, corrections, conclusions. *Bull. Soc. Hist. Nat. Toulouse*, **111** , 1/2 : 126-134

PEDROCCHI - RENAULT, C., 1985. — Los artrópodos epigeos del macizo de San Juan de la Peña (Jaca, Huesca). I. Introducción general a su estudio. *Pirineos*, **124** : 5-52.

SERRA, A. & ASCASO, C., 1990. — Análisis de la composición faunística y variación estacional de los Quilópodos de tres hábitats del Montseny (Cataluña) capturados con trampas de caída. *In* : A. MINELLI, *Proceedings 7th Intern. Congr. Myriapodology.* : 385-401.

Source : MNHN, Paris

Study of Centipede Communities of Three Habitats in the Province of Ciudad Real

Andrès GARCIA RUIZ *& Francisco Javier* SANTIBAÑEZ

Departamento de Biología Animal I (Entomología), Facultad de Ciencias Biológicas, Universidad Complutense
E-28040 Madrid, España

ABSTRACT

The present work is a study of centipede communities of three different habitats in the province of Ciudad Real. These are a poplar grove, a brushwood and rubbish heap. The specimens have been collected by direct sampling and by Berlese funnels. A check-list of the species collected is given. A frequency and abundance analysis have been carried out. The specific richness and diversity have been compared for the three different biocenoses.

RÉSUMÉ

Étude des peuplements de chilopodes de trois types d'habitats dans la province de Ciudad Real (Espagne).

Le présent travail étudie les peuplements de chilopodes de trois types d'habitats de la province de Ciudad Real, en Espagne. Il s'agit d'une peupleraie, d'un fourré de broussailles et d'un monceau de détritus. Le matériel a été récolté par échantillonnage direct et par extraction au Berlese. On donne la liste des espèces collectées, ainsi que leur fréquence et leur abondance. La richesse spécifique et la diversité spécifique ont été estimées de manière comparative au sein des trois biocénoses étudiées.

INTRODUCTION

Usually, when we study the soil fauna, we can observe the great variation that exists between the habitat characteristics and the community of organisms that live there.

The centipedes, because of their affinity to dampness and their restricted tolerance to variations of environment humidity, are easier to find in wet areas.

Consequently, it is rather strange to find populations in places which have a low humidity during the main part of the year.

MATERIAL AND METHODS

Environmental Description:

The area where the present study has been carried out is the Campo de Calatrava, province of Ciudad Real, in the Comunidad de Castilla-La Mancha. The afore mentioned Campo de Calatrava is placed in the Submeseta Sur, between the Montes de Toledo and Sierra Morena. Of note are its old volcanic eruptive defiles caused by isostatics adjustments that took place after the Pontiense. Of note are the volcanic products called "Negrizales" or "Castillejos" as well as some volcanic cones. The soil is dun or red dun of crusty limestone and also mediterranean red soil over siliceous materials

---

GARCIA RUIZ, A. & SANTIBAÑEZ, F. J., 1996. — Study of Centipede Communities of Three Habitats in the Province of Ciudad Real. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 205-208. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

mainly dedicated to agriculture. The climate is mesomediterranean and the vegetation is typical of the corological Luso-Extremadurense province.

Studied Habitats

The studied habitats are three areas in the Campo de Calatrava. The first is a poplar grove with an altitude of 700 m and coordinates UTM 30SVJ5608, characterized by an abundance of dead leaves. The second is a brushwood with an altitude of 869 m and coordinates UTM 30SVH5199, characterized by rocks and scrubs of phytosociological communities as *Cisto clusii - Rosmarinetum* and *Herniario - Teucrietum pumilii*. The third is a rubbish heap, with an altitude of 800 m and coordinates UTM 30SVH4898, characterized by plenty of debris and vegetal nitrophile communities.

Methodology:

The habitats were sampled on one day of the first week of every month during 1987.

Five places in each habitat were chosen and the sampling was made in an area of 3 square meters. Check-lists with the number of specimens of each species were established and the frequency and abundance estimated. In order to compare the structure of each habitat, the following indices were used:

a) SHANNON-WIENER diversity (1949): $H' = - \sum P_i \ln P_i$

This index could be defined as a measure of the specific structure in an ecosystem, based in the number of species present and their relative abundances.

b) Specific richness according to MARGALEFF (1980): $R = (S-1)/\ln N$, where P is the abundance of each species in the habitat ($P_i = N/N$); S is the number of species and N the number of specimens.

RESULTS

Faunistic Composition

On the three studied areas eleven species have been found and can be assembled, according to a biogeographic point of view and to the BROLEMANN (1930) criteria, in the following way:

European species:	*Lithobius lusitanus* Verhoeff, 1925.
Mediterranen species:	*Dignathodon microcephalum* Lucas, 1846.
	Scolopendra cingulata Latreille, 1829.
	Lithobius variegatus rubriceps Newport, 1845.
Holartic species:	*Pachymerium ferrugineum* (C. Koch, 1835).
	Schendyla nemorensis (C. Koch, 1837).
Paleartic species:	*Geophilus carpophagus* Leach, 1814.
Betico-riferenian species:	*Lithobius inermis* L. Koch, 1856.
Endemic species:	*Cryptops hispanus* Brölemann, 1920.
Atlantic species:	*Lithobius pilicornis* Newport, 1845.
Cosmopolitan species:	*Scutigera coleoptrata* (Linné, 1758).

Taxocenoses study

In Tables 1, 2 and 3 we can see the number of specimens belonging to the different species. The total amount of specimens captured was 284 (49 in the poplar grove, 104 in the brushwood and 131 in the rubbish heap).

In the poplar grove, the total number of centipedes is 49 individuals, belonging to 5 different species. The most abundant species is *Pachymerium ferrugineum* (40.81%), after that comes *Lithobius lusitanus* (32.62%) and *Scutigera coleoptrata* (22.44%). In relation to the frequencies we must point out the relative importance of *Lithobius lusitanus* (31.66%) and *Pachymerium ferrugineum* (30.00%).

In the brushwood, the total number of centipedes is 104 individuals, belonging to 8 different species. The most abundant species is *Scolopendra cingulata* (29.80%), after that comes *Lithobius variegatus rubriceps* (24.03%) and *Pachymerium ferrugineum* (12.50%). In relation to the frequencies we must point out the relative importance of *Scolopendra cingulata* (48.33%) and *Lithobius variegatus rubriceps* (38.33%).

Source : MNHN, Paris

TABLE 1. — Poplar grove taxocenoses: number of males (M) and females (H) sampled, proportion among the sexes (M/H), total amount of specimens (NT), frequency (F) and abundance (A) for each species.

	M	H	M/H	NT	F	A
L. pilicornis	2	6	0.33	8	11.66	0.16
L. lusitanus	7	9	0.77	16	31.66	0.32
L. inermis	-	-	-	-	-	-
L. variegatus rubriceps	-	-	-	-	-	-
S. nemorensis	2	0	-	2	3.33	0.04
P. ferrugineum	9	11	0.81	20	30.00	0.40
D. microcephalum	-	-	-	-	-	-
G. carpophagus	-	-	-	-	-	-
C. hispanus	-	-	-	-	-	-
S. cingulata	-	-	-	-	-	-
S. coleoptrata	8	3	2.66	11	16.66	0.22

TABLE 2. — Brushwood taxocenoses: number of males (M) and females (H) sampled, proportion among the sexes (M/H), total amount of specimens (NT), frequency (F) and abundance (A) for each species.

	M	H	M/H	NT	F	A
L. pilicornis	-	-	-	-	-	-
L. lusitanus	8	3	2.66	11	15.00	0.10
L. inermis	-	2	-	2	3.33	0.01
L. variegatus rubriceps	14	11	1.27	25	38.33	0.24
S. nemorensis	-	-	-	-	-	-
P. ferrugineum	7	6	1.16	13	13.33	0.12
D. microcephalum	-	-	-	-	-	-
G. carpophagus	4	7	0.57	11	16.66	0.10
C. hispanus	2	0		2	3.33	0.01
S. cingulata	18	13	1.38	31	48.33	0.29
S. coleoptrata	2	7	0.28	9	11.66	0.08

TABLE 3. — Rubbish heap taxocenoses: number of males (M) and females (H) sampled, proportion among the two sexes (M/H), total amount of specimens (NT), frequency (F) and abundance (A) for each species.

	M	H	M/H	NT	F	A
L. pilicornis	-	-	-	-	-	-
L. lusitanus	12	7	1.71	19	28.33	0.14
L. inermis	-	2	-	-	-	-
L. variegatus rubriceps	13	18	0.72	31	48.33	0.23
S. nemorensis	-	-	-	-	-	-
P. ferrugineum	-	-	-	-	-	-
D. microcephalum	5	9	0.55	14	23.33	0.10
G. carpophagus	9	2	4.50	11	16.66	0.08
C. hispanus	4	3	1.33	7	10.00	0.05
S. cingulata	21	16	1.31	37	58.33	0.28
S. coleoptrata	3	9	0.33	12	18.33	0.09

Source : MNHN, Paris

On the rubbish heap, the total number of centipedes is 131 individuals, belonging to 7 different species. The most abundant species is *Scolopendra cingulata* (28.24%), after that comes *Lithobius variegatus rubriceps* (23.66%) and *Lithobius lusitanus* (14.50%).

In relation to the frequencies we must point out the relative importance of *Scolopendra cingulata* (58.33%) and *Lithobius variegatus rubriceps* (48.33%).

When comparing the results obtained from the three habitats, we must point out that the values for the specific diversity are very similar, being 1.73 for the rubbish heap, 1.68 for the brushwood and 1.46 for the poplar grove. The values for the specific richness are: 1.50 for the brushwood, 1.23 for the rubbish heap and 1.02 for the poplar grove. (Table 4) .

TABLE 4. — Number of species (Nsp), total number of specimens (N), specific richness and diversity in the three studied habitats.

	Nsp	N	Richness	Diversity
Poplar grove	5	49	1.02	1.46
Brushwood	8	104	1.50	1.68
Rubbish heap	7	131	1.23	1.73

CONCLUSION

The most abundant species in the rubbish heap and in the brushwood is *Scolopendra cingulata*, but it seems to be absent in the poplar grove; this is in agreement with its obvious preferences for rocky places.

The second most important species, *Lithobius lusitanus*, is found in the three studied habitats, showing probably a better adaptability to the different conditions of the environment.

Two other species, *Lithobius pilicornis* and *Schendyla nemorensis*, have been found only in the poplar grove and another one, *Lithobius inermis* only in the brushwood. They could be considered as a characteristic for the habitat.

In the present work dealing mainly with a comparison of the three ecosystem types, we have found very similar diversity values but different richness values. However, these results do not show any highly significant differences.

REFERENCES

BROLEMANN, H. W., 1930. — *Eléments d'une Faune des Myriapodes de France. Chilopodes.* [Faune Fr., **25**], Paris, P. Lechevalier : 1-405.

MARGALEF, R., 1980. — *Ecologia.* Barcelona, Omega.

Source : MNHN, Paris

Synanthropisation of the Diplopoda Fauna of Poland

Wojciech B. ***JEDRYCZKOWSKI***

Museum & Institute of Zoology PAS, P.O. Box 1007, ul. Wilcza 64, 00-679 Warszawa, Poland

ABSTRACT

More than 5,000 specimens of millipedes belonging to 40 species have been collected and analysed from synanthropic sites in Poland. Six main zoogeographical elements were distinguished. The European element was represented by 26 species. Four ecological elements were distinguished, from which synanthropic species were most abundant in Warsaw (13 species).

RÉSUMÉ

Anthropisation de la faune de diplopodes de Pologne.

Plus de 5000 spécimens de diplopodes appartenant à 40 espèces ont été collectés dans des sites anthropisés de Pologne et étudiés. Six composantes zoogéographiques principales ont été distinguées. La composante européenne est représentée par 26 espèces. On a distingué par ailleurs 4 composantes écologiques, pour lesquelles les espèces synanthropiques étaient plus abondantes à Varsovie (13 espèces).

INTRODUCTION

Most faunistic and ecological publications are dedicated to national parks, protected areas and other natural environments. Only a few deal with habitats that have been created or modified by human activities.

Towns, as a typical example of a new habitat created by man for man, are interesting places for studying processes of plant and animal colonisation, ecological adaptation and behavioural changes among native fauna. Within towns the process of synanthropisation occurs, which leads to the colonisation of urban areas by species with different ecological specialisations. These species and groups of species are able to overcome the ecological barriers and colonize the direct environment of man. In this way they enrich the ecosystem, forming at the same time new values for people themselves. Factors controlling these processes and influencing the development of fauna in "urbicœnoses", should be recognized as of great importance for making forecasts as to evaluate them in the phase of planning housing estates, and to control them in the most convenient way for man and the ecosystem.

MATERIAL AND METHODS

During a 6 year period, 1974 - 1979, faunistic and ecological studies on the animals inhabiting towns in Poland have been carried out at the Institute of Zoology PAS in Warsaw. These studies were aimed at answering a number of theoretical and practical questions concerning the state and the role of the fauna in urban environment (TROJAN, 1981).

JEDRYCZKOWSKI, W. B., 1996. — Synanthropisation of the Diplopoda fauna of Poland. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 209-212. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

So far, most of the studies on millipedes (Diplopoda) in Poland have been carried out in natural habitats. Relatively few workers were interested in habitats transformed by human activities. The research project mentioned above created opportunities to study the influence of synanthropic factors on the millipede fauna on a large scale. Warsaw was treated as a model of synanthropic processes which can take place everywhere.

RESULTS

During the study period more than 5,000 specimens of millipedes belonging to 40 species were collected and analysed from synanthropic sites in Poland. Six main zoogeographical components were distinguished. The European component was represented by 26 species. Four ecological components were distinguished, from which synanthropic species were most abundant in Warsaw (13 species).

Habitat types

The studied localities can be grouped into the following five main types of habitats (NOWAKOWSKI, 1981) (Fig. 1).

FIG 1. — Location of the study plots in Warsaw. 1 - suburban areas; 2 - parks; 3 - housing estates; 4 - lawns; 5 - greenhouses.

1. Suburban areas. An urban wood - a nature reserve - with a surface area of over 130 ha. It is located on the Vistula river left bank, dominated by a lime-oak-hornbean forest (*Tilio-Carpinetum*), in places modified towards a secondary mixed forest. The woods are inhabited by

Source : MNHN, Paris

10 species of millipedes (Table 1). Six of them: *Glomeris connexa, Heteroporatia bosniensis, Nemasoma varicorne, Julus terrestris, Leptoiulus proximus* and *Ophiulus fallax* were found only in this kind of habitat. They are not able to enter the centre of town.

2. Parks. There are several old parks in Warsaw covered by a variety of greens, with patches of preserved forests and an area of up to 86 ha. They create good conditions for eleven species of millipedes living there. Most of them belong to synanthropic species such as *Cylindroiulus caeruleocinctus* and *Kryphioiulus occultus* which achieve their abundance. Some of the natural environment species can also live there.

3. Greens of housing estates. This type of habitat can hardly be characterized, since it varies in size and floristic composition. The only factors they share are great intensity of cultivation and very strong penetration by people and domestic animals. In such conditions only four synanthropic species of millipedes can exist.

4. Lawns and courtyard greens. In general, these types of habitats do not exceed 250 m^2 in surface area. The lawns, especially along streets, are heavily contaminated with salt and subject to frequent drought conditions. The species composition is poor and consist of four species only.

5. Greenhouses. These are the most artificial of all types of habitats which have been created by human activity. They have high and constant temperature as well as humidity. Diplopods dwelling there are typical synanthropic species which origin from tropics. In Warsaw, seven species of millipedes have been recorded from greenhouses. Three of them (*Ophiodesmus albonanus, Oxidus gracilis* and *Cylindroiulus truncorum*) live exclusively in this type of habitat.

TABLE 1. — Check-list of the *Diplopoda* occurring in Warsaw. Numbers of specimens collected.

	Suburban areas	Parks	Housing estates	Lawns	Green-houses	Total
G. connexa	13					13
H. bosniensis	40					40
B. superus	3	27	7	1		38
P. inconstans		9	5	36		138
P. complanatus	28	1				29
O. albonanus					1	1
O. gracilis					7	7
B. guttulatus		32			3	35
B. tenuis		1				1
C. palmatus		1			7	8
N. varicorne	1					1
P. fuscus	1	1				2
N. venustus		5				5
C. frisius	52	17	29	10	2	110
C. truncorum					8	8
C. caeruleocinctus		242	3	57		302
K. occultus		449			2	451
J. terrestris	15					15
L. proximus	11					11
O. fallax	8					8
U. foetidus	4	94	6	6		110
P. germanicum	35					35
Total	211	967	50	110	30	1368

Source : MNHN, Paris

Species groups

Analysing the species composition of the millipedes fauna of synanthropic habitats, we can conclude that the Diplopoda occurring in Warsaw belong mostly to the species showing high ecological amplitudes and due to this they are able to inhabit several urban habitats (JEDRYCZKOWSKI, 1982). From an ecological point of view, they can be divided in three groups depending on the transformation of environment.

1. The first group consists of native species having a great ecological tolerance which are able to enter into suburban greens, but are not able to live in the central part of town. It is represented by *G. connexa, H. bosniensis, P. complanatus, N. varicorne, P. fuscus, J. terrestris, L. proximus* and *O. fallax*.

2. The second group represents mainly synanthropic species, which originates mainly from the south and west part of Europe, they dwell in parks and estate greens but occasionally can inhabit some natural or seminatural habitats. As representatives of this group, *P. inconstans, C. latestriatus* (*=frisius*) and *C. caeruleocinctus* can be mentioned.

3. The third group is build up by species of tropical or unknown origin. Usually, they live in a variety of greenhouses (where they can achieve a high numbers of individuals) sometimes they can live out of buildings for a long period, especially when winters are mild.

DISCUSSION

The species diversity and the number of specimens occurring in towns depend on the age and type of the inhabited greens. The highest specific richness occurs in old parks, with large green patches, dense lawns with shrubs and where the litter is well preserved, providing shelter for animals.

A high percentage of millipedes belong to the group of expansive species, which have successfully colonized almost the whole Europe. The high ecological amplitude enables them to adapt to changing habitat conditions. Synanthropic species, especially those belonging to the genus *Cylindroiulus*, native of the Mediterranean, are a good example here. Urban pressure firstly eliminates the species associated with forests and thickets. They still can live in the suburbs but they do not colonize parks and housing estates.

REFERENCES

JEDRYCZKOWSKI, W., 1982. — Millipedes (Diplopoda) of Warsaw and Mazovia. *Memorabilia Zool. Warszawa*, **36** : 253-261.

NOWAKOWSKI, E., 1981. — Physiographical Characteristics of Warsaw and the Mazovian Lowland. *Memorabilia Zool. Warszawa*, **34** : 13-31.

TROJAN, P., 1981. — Urban Fauna: Faunistic, Zoogeographical and Ecological Problems. *Memorabilia Zool. Warszawa*, **34** : 3-12.

Source : MNHN, Paris

Chilopoda of Urban Greens in Warsaw

Jolanta WYTWER

Muzeum i Instytut Zoologii PAN ul. Wilcza 64, 00-679 Warszawa, Poland

ABSTRACT

A total of twelve Chilopoda species have been registered in three types of urban greens in Warsaw: seminatural wooded areas, big parks and streetside lawns. The common core of Chilopoda communities in all three types of urban greens contained six eurytopic species, with *Lithobius microps* as the most abundant. There were noticeable changes in the dominance structure of the epigeic part of Chilopoda communities related to urban greens types. *Lithobius microps* gradually replaced *Lithobius forficatus*, which is a very abundant species in wooded areas but relatively scarce in street lawns.

RÉSUMÉ

Chilopodes des espaces verts urbains de Varsovie.

Les peuplements de chilopodes ont été étudiés dans trois types d'espaces verts urbains à Varsovie : des boisements semi-naturels, de grands parcs et des pelouses situées près des chaussées. Le matériel a été récolté au cours de la période 1988-1990 à l'aide d'échantillons de sol et de pièges Barber. Au total, on a récolté douze espèces de chilopodes dont le plus grand nombre se trouve, en moyenne, dans les boisements (5,8), alors que la plus faible richesse spécifique est enregistrée dans les pelouses (4,5). Dans les trois types d'espaces verts, les six espèces communes apparaissent avec une constance dépassant 50% et constituent environ 2/3 de la composition taxonomique du peuplement. Ce sont : *Lithobius microps*, *Necrophloeophagus flavus*, *Schendyla nemorensis*, *Geophilus electricus*, *Strigamia crassipes* et *Lithobius forficatus*. Dans les trois types d'espaces verts *L. microps* prédomine. L'analyse des structures dominantes des peuplements de chilopodes à l'aide des indices de Morisita, de l'homogénéité de domination et de rangs, a montré l'existence de changements dépendant du degré d'anthropogénisation des espaces verts urbains. Dans le compartiment épigéique, on a observé que l'importance relative de *L. microps* s'accroît au détriment de *L. forficatus*, qu'il remplace progressivement.

INTRODUCTION

Studies of Chilopoda conducted over the last several decades in many European cities, e.g. in Copenhagen (ENGHOFF, 1973), Kiel (TISCHLER, 1980), Göteborg (ANDERSSON, 1983) and Rome (ZAPPAROLLI, 1992) indicate that urban Chilopoda communities are characterized by high proportions of alien species and a significant degree of faunal diversification. Striking differences in the abundance of Chilopoda are noted between individual study sites. Equally unusual is the occurrence of many species as single specimens, a phenomenon which was particularly conspicuous in a quantitative study carried out in Bonn Bad-Godesberg (FRÜND, 1989; SCHULTE *et al.* 1989). We do not know yet, however, whether Chilopoda communities inhabiting different types of urban greens belong to one or more faunal associations, in other

WYTWER, J., 1996. — Chilopoda of Urban Greens in Warsaw. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 213-220. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

words, whether the differences in species composition and species abundance are accidental or testify to their individual characters. The following paper analysing Chilopoda of urban greens of Warsaw attempts to provide an answer.

MATERIAL AND METHODS

Sampling areas

The research was carried out in 13 sampling areas that represented 3 types of urban greens (Fig. 1):

1. *wooded areas* with ground cover growing spontaneously. Such areas are not subject to regular horticultural practices (e.g. digging over or raking). They are located along the edge of the erosion valley of the Vistula river that cuts across the area of Warsaw. Areas W1 and W5, situated on the outskirts of Warsaw, represent the linden-oak-hornbeam forest in phytosociological terms. Areas W1-W4 are characterized by a high inclination angle. Area W5 is the only one situated on the upper erosion terrace within the *Lasek Bielański* reserve.

2. *park lawns* are subject to regular horticultural practices i.e. lawn trimming and litter raking. Areas P1-P4 are located within larger park areas at least 50 meters away from a roadway.

3. *street lawns* (S1-S4) are situated in the immediate vicinity of busy arterial roads.

Sampling methods

Two sampling methods were used for collecting Chilopoda:

1) BARBER's pitfall traps. 10 traps were placed in each area. The animals were collected once a fortnight from April 1988 to March 1990;

2) soil samples with an area of 0.1 m^2, taken down to a depth of about 25 cm. 3 or 5 samples were taken in May and September 1990. 32 soil samples were taken altogether in each of the three types of urban greens. The specimens were sorted by hand.

FIG. 1. — Location of the urban greens in Warsaw.

Source : MNHN, Paris

RESULTS

Species composition

12 species of centipedes were recorded from urban greens in Warsaw (Table 1). The greatest numbers of species were found in wooded areas - 5.8 on average, compared to 5.0 in park lawns and only 4.5 in street lawns. As far as the number of species is concerned, the Chilopoda communities of urban greens of Warsaw are not basically different from forest Chilopoda communities of Central Europe, where 5-10 species are usually recorded (THIELE, 1956; ALBERT, 1979; BECKER, 1982; FRÜND, 1987; KACZMAREK, 1989; WYTWER, 1990, 1992).

TABLE 1. — Species of Chilopoda in urban greens of Warsaw.

Nº	Species	wooded areas					parks				street lawns			
		W1	W2	W3	W4	W5	P1	P2	P3	P4	S1	S2	S3	S4
1	*Lithobius forficatus* (L.)	+	+	+	+		+	+			+			
2	*Lithobius melanops* Newport								+					
3	*Lithobius mutabilis* L. Koch	+				+								
4	*Lithobius crassipes* L. Koch				+									
5	*Lithobius microps* Meinert	+	+	+	+	+	+	+	+	+	+	+	+	+
6	*Lamyctes fulvicornis* Meinert								+					
7	*Necrophloeophagus flavus* (De Geer)	+	+	+	+	+	+	+	+	+	+	+		+
8	*Clinopodes linearis* (C. Koch)							+						
9	*Geophilus electricus* (L.)	+	+	+	+		+		+	+	+	+		+
10	*Brachygeophilus truncorum* (Berg. & Mein.)													+
11	*Strigamia crassipes* (C. Koch)	+	+	+	+	+	+				+	+		
12	*Schendyla nemorensis* (C.Koch)	+		+		+	+	+		+	+	+	+	+
	Number of species	7	5	6	6	5	6	5	5	4	6	5	2	5

The following six species occurred in all the three types of urban greens and were consequently considered to be common: *Lithobius forficatus, Lithobius microps, Necrophloeophagus flavus, Geophilus electricus, Strigamia crassipes* and *Schendyla nemorensis*. The similarity of the species composition of such communities, expressed as the MARCZEWSKI-STEINHAUS index (MARCZEWSKI & STEINHAUS, 1958) oscillates closely around 60% (Table 2).

TABLE 2. — Similarity (in percent) of species composition in Chilopoda communities in urban greens of Warsaw according to MARCZEWSKI-STEINHAUS index (MS).

Type of urban greens	MS
wooded areas x parks	54.5
parks x street lawns	60.0
wooded areas x street lawns	66.7

In order to determine the degree of fidelity of individual Chilopoda species to the urban green habitat, a constancy analysis was performed using TISCHLER's method (TISCHLER, 1949). The analysis revealed the presence of two groups of species (Fig. 2). The first group is characterized by an index of constancy above 0.5 and is composed of the same six species listed above as common to communities of all the three types of urban greens. The other group consists of species with much lower values of constancy (below 0.2).

It can be assumed that the Chilopoda species occurring in all the three types of urban greens and characterized by high constancy indices form the core of the Chilopoda communities

Source : MNHN, Paris

of urban greens. The species from the other group are found occasionally in single sites and function as accessory elements of the community.

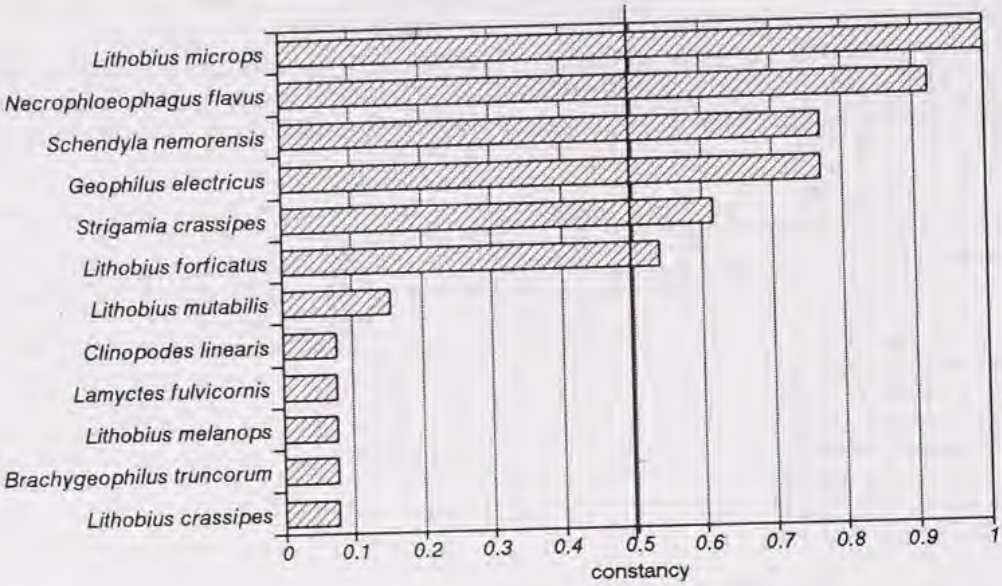


FIG. 2. — Constancy of occurence of individual Chilopoda species in the urban greens of Warsaw.

The structure of dominance

The combining of the two methods of sampling helped to clarify and compare the dominance structure of Chilopoda communities inhabiting the surface and the deeper layer of soil (Fig. 3a, b). The similarity of dominance relationships are well reflected by MORISITA's index - MO (HORN, 1966) and the index of homogeneity - HD (RIEDL, 1963). When the centipede fauna of the deeper layers of soil is analysed, the values of both indices are relatively high - above 90 and 70% (Table 3). Therefore it can be assumed that the structure of this part of the community is uniform in all types of urban greens in Warsaw.

TABLE 3. — Similarity (in percent) of dominance structure of Chilopoda communities. MO: index of similarity (MORISITA index); HD: index of homogeneity, based on the species dominance structure; HR: index of homogeneity, based on the ranks of dominance structure.

Method	Type of urban greens	MO	HD	HR
soil	wooded areas x parks	98.5	80.2	83.1
samples	parks x street lawns	96.0	73.8	74.0
	wooded areas x street lawns	98.1	78.2	78.1
pitfall	wooded areas x parks	79.4	51.0	83.9
traps	parks x street lawns	75.2	42.0	41.2
	wooded areas x street lawns	55.3	32.0	36.9

The similarity of the dominance structures of the epigean parts of Chilopoda communities of different types of greens is expressed by much lower values of the both indices - below 79 and 51%. This is mostly caused by a decrease in the proportion of *Lithobius forficatus* in parks and street lawns (Fig. 3b). This species is being gradually replaced by *Lithobius microps*.

Source : MNHN, Paris

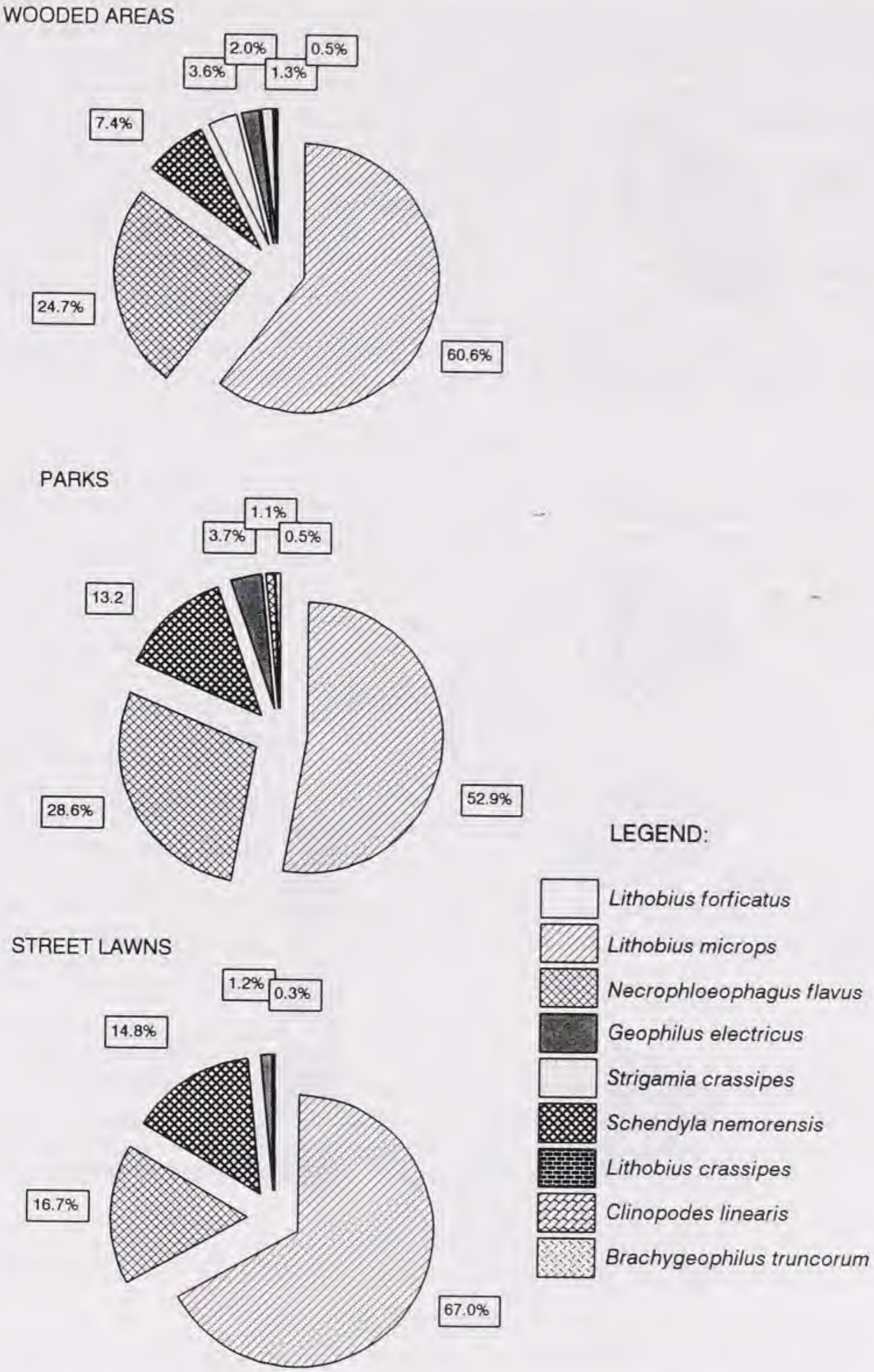


FIG. 3a. — Percentage contribution of Chilopoda species in the soil sample material.

Source : MNHN, Paris

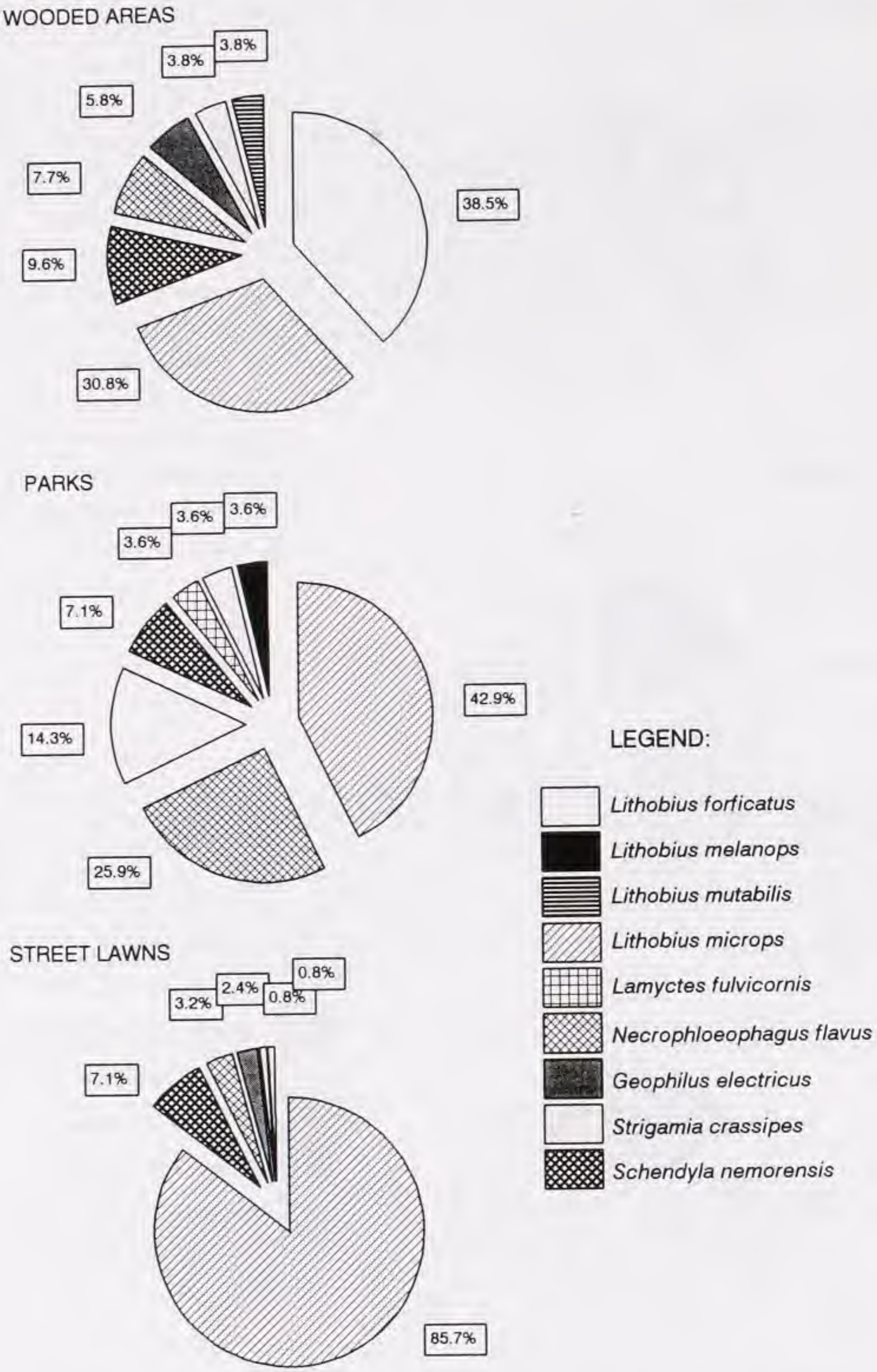


FIG. 3b. — Percentage contribution of Chilopoda species in the pitfall trap material.

Source : MNHN, Paris

The structure of dominance of the epigean component of Chilopoda communities is undergoing major changes. This is not, however, a sign of a change of the dominance model of Chilopoda communities in various types of urban greens. The degree of overlap of the dominance models has been determined by means of a homogeneity coefficient, where dominance models arranged according to the ranks (shares) of species provided a basis for the analysis. Owing to this similarity of dominance relations could be analysed irrespective of the fact what species takes succeeding position. The values of "ranks homogeneity coefficient" (HR) indicate that the communities of wooded areas and parks have a very similar dominance model (Table 3). It differs, however, from the dominance model of Chilopoda communities of the street lawns, particularly in the epigean layer, where the dominance of *Lithobius microps* is very strong. Therefore, the restructuring of Chilopoda communities under marked urbanizing pressure, which is currently taking place in urban greens, affects above all else the epigean forms. Species inhabiting deeper layers of soil are able to preserve structural relations in an almost intact form, the only modifications being due to the exchange of accidental species.

DISCUSSION

Except for *Strigamia crassipes*, all the species which form the core of Chilopoda communities of urban greens are known to be eurytopic and occur in most of the European cities where centipede fauna has been studied. The occurrence of *S. crassipes* in urbanized environments could have been underestimated so far since this species reaches its maximum of abundance in winter (BARBER & KEAY, 1988) and is therefore not included in faunal studies of Chilopoda. Most individuals of this species were collected by pitfall trapping in early spring (end of winter) and late autumn.

The accidental species which have been found in parks and street lawns are known to spread by means of horticultural practices in artificial man-made environments as it is the case with *Clinopodes linearis* and *Brachygeophilus truncorum*. On an other hand, wooded areas and old parks in the centre of the town are often abundant in species that once inhabited the natural habitats, such as *Lithobius crassipes, Lithobius melanops* and *Lamyctes fulvicornis* which are able to remain in a synanthropic environment. However, they are not able to occur on the street lawns because they belong to the epigean part of the community which is undergoing marked structural transformations. An exclusively forest species, such as *Lithobius mutabilis*, has survived only in wooded areas on the outskirts of the city (linden-oak-hornbeam forest) as it is a constant and important element in Chilopoda communities of this habitat type in the Mazovian Lowland (WYTWER, 1990).

CONCLUSION

One type of centipede community can be considered to occur in urban greens of Warsaw, its core consists of 6 eurytopic species that do not avoid "synanthropised" environments. The other species are distributed randomly among various sites where they function as accessory species. The influence of the urban environment on the structure of Chilopoda communities manifests itself in marked transformation of the epigean part of the community.

ACKNOWLEDGEMENT

I am grateful to prof. dr hab. P. TROJAN for helpful advice and critical review of the manuscript.

REFERENCES

ALBERT, A. M., 1979. — Chilopoda as part of the predatory macroarthropod fauna in forests: abundance, life-cycle, biomass and metabolism. *In* : M. CAMATINI, *Myriapod Biology*. London, Academic Press : 215-231.

ANDERSSON, G., 1983. — The chilopoda fauna in the vicinity of Göteborg - a comparison between collecting results obtained in the 1920s and the 1970s years. *Acta ent. fenn. Helsinki*, **42** : 9-14.

Source : MNHN, Paris

BARBER, A. D. & KEAY A. N., 1988. — *Provisional atlas of the centipedes of the British Isles*. Huntington, Biological Records Centre, 127pp.

BECKER, J., 1982. — Hundertfüssler (Chilopoda) des Bausenbergs und der östliche Eifel. *Decheniana*, **27** : 76-86.

ENGHOFF, H., 1973. — Diplopoda und Chilopoda from suburban localities around Copenhagen. *Vidensk. Meddr dansk naturh. Foren.*, **136** : 43-48.

FRÜND, H. C., 1987. — Raumliche verteilung und Koexistenz der Chilopoden in einem Buchen-Altebestand. *Pedobiologia*, **30** : 19-29.

FRÜND, H. C., 1989. — Untersuchungen zur Biologie städtischer Böden. 5. Epigäische Raubarthropoden. *Verh. Ges. ökol.*, **18** : 201-209.

HORN, H. S., 1966. — Measurement of "overlap" in comparative ecological studies. *Am. Nat.*, **100** : 410-424.

KACZMAREK, J., 1989. — Pareczniki (Chilopoda) wybranego lasu gradowego Wielkopolski na przykæadzie Rezerwatu "Jakubowo". *Fragm. faun.*, **32** : 369-379.

MARCZEWSKI, E. & STEINHAUS, H., 1958. — On a certain distance of sets and corresponding distance of function. *Coll. Math.*, **6** : 319-327.

RIEDL, R., 1963. — Probleme und Methoden der Erforschung des litoralen Benthos. *Verh. d. Dtsch. Zool.*, **Suppl. 26** : 505-567.

SCHULTE, W. *et al.* 1989. — *Untersuchungen zur Bodenökologischen Bedeutung von Freiflächen im Stadtbereich*. Forschungsbericht des Bundesministerium für Forschung und Technologie, Hamburg, 200pp.

THIELE, H. V. U., 1956. — Die Tiergesellschaften den Bodenstreu in den verschiedenen Waldtypen des Niederbergischen Landes. *Z. angew. Ent.*, **39** : 316-369.

TISCHLER, W., 1949. — *Grundzüge der terrestrischen Tierökologie*. Berlin, F. Vieweg & Sohn, 220pp.

TISCHLER, W., 1980. — Asseln (Isopoda), Tausendfüssler (Myriapoda) eines Stadtparks im Vergleich mit der Umgebung der Stadt: zum Problem der Urbanbiologie. *Drosera*, **80** : 41-52.

WYTWER, J., 1990. — Chilopoda of linden-oak-hornbeam (*Tilio-Carpinetum*) and thermophilous oak forests (*Potentillo albae-Quercetum*) of the Mazovian Lowland. *Frag. faun.*, **34** : 73-94.

WYTWER, J., 1992. — Chilopoda communities of the fresh pine forests of Poland. *In* : [E. MEYER, K. THALER & W. SCHEDL, *Advances in Myriapodology*.] *Ber. nat.-med. Verein. Innsbruck*, **Suppl. 10** : 205-211.

ZAPPAROLI, M., 1992. — Centipedes in urban environments: records from the city of Rome (Italy). *In* : [E. MEYER, K. THALER & W. SCHEDL, *Advances in Myriapodology*.] *Ber. nat.-med. Verein. Innsbruck*, **Suppl. 10** : 231-236.

Source : MNHN, Paris

Centipedes of Poznan Town (Poland)

Malgorzata LESNIEWSKA

Zaklad Zoologii Ogólnej, Uniwersytet im. Adama Mickiewicza, ul. Fredry 10, 61 - 701 Poznan, Polska

ABSTRACT

Quantitative studies on the centipedes of Poznan have been carried out since 1988. The studies cover areas with different degrees of transformation by man, like parks, squares, cemeteries, allotment gardens, dumping grounds, etc. As a result of these studies, the occurence of 18 centipede species has been found, constituting 33% of the Chilopodan fauna of Poland. Among the most frequent species found in Poznan, are: *Lithobius forficatus* and *Lithobius microps* from the order Lithobiomorpha and *Necrophloeophagus flavus* and *Schendyla nemorensis* from the order Geophilomorpha. The occurence of *Haplophilus subterraneus* has been registered for the first time in Poland. The studies are to be continued.

RÉSUMÉ

Chilopodes de la ville de Poznan (Pologne).

Les chilopodes de Poznan sont étudiés depuis 1988. Les recherches sont effectuées sur des sites diversement transformés par les activités humaines, tels que parcs, squares, cimetières, espaces verts, jardins, amas d'ordures, etc. Nous avons constaté la présence de 18 espèces, représentant 33% de la faune des chilopodes de Pologne. Parmi les espèces les plus fréquentes, on note : *Lithobius forficatus* et *Lithobius microps* pour l'ordre Lithobiomorpha, *Necrophloeophagus flavus* et *Schendyla nemorensis* pour l'ordre Geophilomorpha. L'espèce *Haplophilus subterraneus* a été répertoriée pour la première fois en Pologne.

INTRODUCTION

In the European myriapodological literature of the recent years, we can find some works describing the urban centipede fauna including -among others- Copenhagen (ENGHOFF, 1973), Göteborg (ANDERSSON, 1983) or Rome (ZAPPAROLI, 1990a, b).

In the polish literature, there are no works of this type so far, although in recent years, three masters theses were prepared referring to centipedes of Poznan and one study devoted to this group of animals is under preparation in Warsaw (WYTWER, this volume).

This work presents preliminary results of qualitative studies carried out since 1988 in Poznan.

STUDY AREA

Poznan is the largest town in Wielkopolska, founded in the 9th century. It is situated on Warta river at the altitude of 52-154 m above sea level, covering 261.3 km^2, with 589.7 thousands inhabitants. The climate is moderately continental . The annual rainfall is the lowest in Poland, below 500 mm. The annual isotherm is 8.5°C. The winters are

LESNIEWSKA, M., 1996. — Centipedes of Poznan town (Poland). *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 221-224. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

mild (-2°C) and summers are warm (18°C). The growing season lasts 210-220 days. The relief is characterised by Baltic glaciation. The soils include podzolic and brown soils.

Poznan is a city of International Trade Fairs, visited since 1921 by business men presenting their merchandise from all over the world. This may exert an influence on the spreading of some plant and animal species.

MATERIAL AND METHODS

The following results refer to qualitative studies carried out in 1988. The material was collected by direct sampling of specimens under stones, timber, stems, etc. and by the use of litter sieving.

Samples were taken in 33 localities (in parks, cemeteries, squares, dumping grounds, etc.). These localities were divided into 3 categories, taking into consideration primarily their degree of influence by the activity of man.

Category I. - areas completely transformed by man and his continuous interference (e.g. railways, embankments, wild dumping grounds, roadsides).

Category II. - areas partially changed, covered with vegetation maintained by man (squares, cemeteries, allotment gardens).

Category III. - areas subject to the least interference (mainly less cultivated parks and afforested areas on town edges).

Each locality was inspected at least 5 times. The material was collected by up to three people. During 5 years (1988 - 1992), 1628 individuals belonging to Chilopoda orders were collected. The results include also some materials collected for a masters theses.

RESULTS

During the studies on the area of Poznan, the occurence of 18 centipede species have been found, including 11 belonging to the Geophilomorpha, 1 to the Scolopendromorpha and 6 to the Lithobiomorpha. For the first time, the two species *Clinopodes linearis* and *Clinopodes flavidus* have been registered for the fauna of Wielkopolska, and the occurrence of *Haplophilus subterraneus* has been found for the first time for the fauna of Poland. The most frequently occurring species include two lithobiomorphs: *Lithobius microps* and *Lithobius forficatus* and two geophilomorphs: *Necrophloeophagus flavus* and *Schendyla nemorensis* (Table I).

TABLE 1. — The occurence of centipedes in particular habitat types (number of localities).

	LIST OF IDENTIFIED SPECIES	Category I	Category II	Category III	Frequency
1	*Haplophilus subterraneus* (Shaw)	0	0	1	3%
2	*Schendyla nemorensis* (C. L. Koch)	5	6	5	48%
3	*Strigamia crassipes* (C. L. Koch)	0	5	2	21%
4	*Strigamia acuminata* (Leach)	0	0	1	3%
5	*Pachymerium ferrugineum* (C. L. Koch)	0	2	0	6%
6	*Clinopodes linearis* (C. L. Koch)	2	1	1	12%
7	*Clinopodes flavidus* C. L. Koch	0	2	0	6%
8	*Geophilus electricus* (Linné)	4	5	1	30%
9	*Geophilus proximus* C. L. Koch	1	1	0	6%
10	*Necrophloeophagus flavus* (De Geer)	4	5	7	48%
11	*Brachygeophilus truncorum* (Bergsö & Meinert)	4	3	2	27%
12	*Cryptops hortensis* Leach	0	2	6	24%
13	*Lithobius forficatus* (Linné)	8	7	9	73%
14	*Lithobius erythrocephalus* C. L. Koch	0	2	4	18%
15	*Lithobius melanops* Newport	1	3	4	24%
16	*Lithobius crassipes* L. Koch	1	3	5	27%
17	*Lithobius curtipes* C. L. Koch	0	0	3	9%
18	*Lithobius microps* Meinert	9	11	10	90%
	Number of species	10	14	15	

Remarks on the species (in decreasing frequency order)

1. *Lithobius microps* Meinert - European, eurytopic species, showing a tendency to occur very frequently in man-made habitats (EASON, 1964; ENGHOFF, 1973; ANDERSSON, 1983;

Source : MNHN, Paris

BARBER, 1985; LEWIS, 1985; ZYCH, 1989). In Poznan, this is the most frequent and numerous species in all categories of localities (Table I).

2. *Lithobius forficatus* (Linné) - W-Palaearctic, eurytopic species. In Poland, this is the most common representative of the genus (KACZMAREK, 1979, 1980). In Poznan it is very frequent everywhere.

3. *Necrophloeophagus flavus* (De Geer) - Palaearctic, eurytopic species. In Poland, it is present in natural and synanthropic habitats. The records from Poznan have been collected in all categories of localities (Table I).

4. *Schendyla nemorensis* (C. L. Koch) - W-Palaearctic, woodland species. In Poland, it is common in different woodlands but also in artificial habitats.

5. *Geophilus electricus* (Linné) - European, eurytopic species, with a tendency to be more numerous in urban localities. According to KACZMAREK (1980), in Poland it is rare and not numerous. In Poznan it seems to occur in habitats partially and completely changed by man (Table I).

6. *Lithobius crassipes* L. Koch - European, woodland species. In Poland, it is common in natural and synanthropic localities. In Poznan the highest proportion of records has been collected in areas of the category III (Table I).

7. *Brachygeophilus truncorum* (Bergsö & Meinert) - European, eurytopic species. In Poland, common in woodlands in the west part of the country (KACZMAREK, 1980). In Poznan, it has been found in all habitats sampled.

8. *Lithobius melanops* Newport - Palaearctic, woodland species. In Poznan, it has been collected in all categories of habitats but the largest proportion of records has been obtained from woody areas.

9. *Cryptops hortensis* Leach - Palaearctic, eurytopic species, in some regions synanthropic. The records from Poznan have been collected especially from less cultivated parks and woody areas (Table I).

10. *Strigamia crassipes* (C. L. Koch) - Palaearctic, eurytopic species. In Poland, it occurs in woodlands and synanthropic areas.

11. *Lithobius erythrocephalus* C. L. Koch - European, eurytopic species. In Polish lowlands, apart from *L. forficatus* and *L. mutabilis* - the most common representative of the genus. In urban localities, it is rare (KACZMAREK, 1980). In Poznan, it is mostly found in afforested areas on town outskirts (Table I).

12. *Clinopodes linearis* (C. L. Koch) - European, eurytopic species, in Poland mainly in synanthropic areas.

13. *Lithobius curtipes* C. L. Koch - European, woodland species. In Poland, it occurs in urban localities (KACZMAREK, 1980). The records from Poznan have been collected only from wooded areas (Table I).

14. *Geophilus proximus* C. L. Koch - European, woodland species. In Poznan, it has been recorded in areas changed by man.

15. *Clinopodes flavidus* C. L. Koch - Palaearctic, woodland species. In Poland, it is very rare. In Poznan, it has been collected for the first time for Wielkopolska.

16. *Pachymerium ferrugineum* C. L. Koch - Holarctic, eurytopic species. In Poland (and in Poznan), it occurs outside forests, in warm, dry places.

17. *Strigamia acuminata* (Leach) - Holarctic, woodland species. In Poznan, the records are from one old park.

18. *Haplophilus subterraneus* (Shaw) - an introduced species new for the fauna of Poland. The records (3 specimens) are an old park (LESNIEWSKA & WOJCIECHOWSKI, 1992).

Therefore, one may say that, from a zoographic point of view, the centipedes of Poznan represent the following elements:

- European - 8 (47%),
- Palaearctic - 7 (41%),

Source : MNHN, Paris

- Holarctic -2 (12%).

On an other hand, due to ecological requirements, the following species categories can be distinguished:

- eurytopic -10 (59%),
- woodland -7 (41%).

(*Haplophilus subterraneus* has not been taken into account.)

It has been found that the fauna of Poznan is poorer by 15 species than the Wielkopolska region where it is situated. The centipedes of Poznan represent 55% of the fauna of Wielkopolska and 33% of the fauna of Poland. Quantitative studies are under investigation.

CONCLUSION

The present results should be regarded as preliminary ones because quantitative studies are still under investigation. Nevertheless, the species composition and data referring to the frequency of occurrence are similar to those obtained by other authors investigating on the Chilopoda fauna of European towns (ENGHOFF, 1973; ANDERSSON, 1983; ZAPPAROLI, 1990 a, b).

REFERENCES

ANDERSSON, G., 1983. — The Chilopod fauna in the vicinity of Göteborg - a comparison between collecting results obtained in the 1920s and the 1970s. *Acta Entomol. Fenn.*, **42** : 9-14.

BARBER, A. D., 1985. — Distribution patterns in British Chilopoda. *Bijdr. Dierk.*, **55** : 16-24.

EASON, E. H., 1964. — *Centipedes of British Isles.* London, F. Warne& C° Ltd, 294 pp.

ENGHOFF, H., 1973. — Diplopoda and Chilopoda from suburban localities around Copenhagen, *Vidensk. Meddr dansk nathur. Foren.*, **136** : 43 - 48.

KACZMAREK, J., 1979. — *Pareczniki (Chilopoda) Polski.* Poznan, UAM.

KACZMAREK, J., 1980. — *Katalog fauny Polski. Pareczniki.* Czêœæ XIV.

LESNIEWSKA, M. & WOJCIECHOWSKI, J., 1992. — *Haplophilus subterraneus* (Shaw, 1794) (Chilopoda, Geophilomorpha) - nowy dla fauny Polski przedstawiciel pareczników. *Przeg. Zool.*, **XXXVI,** 1 - 4 : 133 - 136.

LEWIS, J. G. E., 1985. — Centipedes enterning houses with particular reference to *Geophilus carpophagus* Leach. *Ent. mon. Mag.*, **121** : 257-259.

ZAPPAROLI, M., 1990a. — Centipedes in Urban Environments: Records from the City of Rome (Italy). *Ber. nat. - med. Verein Innsbruck.* **Suppl 10** : 231 - 236.

ZAPPAROLI, M., 1990b. — Chilopodi di ambienti urbani e suburbani della citta di Roma. *Boll. Ass.Romana Entomol.*, **44** : 1 - 12.

ZYCH, M., 1989. — Uwagi o wystêpowaniu *Lithobius microps* Meinert (Chilopoda, Lithobiomorpha). *Przegl. Zool.*, **XXXIII** : 332-335.

Source : MNHN, Paris

Contribution à la connaissance des lithobiomorphes (Chilopoda) de la région palestinienne

Stefan NEGREA *& *Zachiu* MATIC **(†)

* Institut de Spéologie "E. Racovitza", Bucarest, Romania
** Lab. Zoologie, Fac. Biol. Geol., Univ. Cluj-Napoca, Romania

RÉSUMÉ

Se basant sur le matériel de lithobiomorphes Henicopidae et Lithobiidae rapporté d'Israël en 1990 par S. NEGREA et coll., les auteurs présentent de nouvelles données systématiques, écologiques et zoogéographiques concernant les espèces appartenant aux genres *Lamyctes*, *Eupolybothrus* et *Monotarsobius*. Une espèce nouvelle : *Monotarsobius teldanensis* n. sp. est décrite. Le travail s'achève par des remarques sur la faune de lithobiomorphes de la région palestinienne.

ABSTRACT

Contribution to the knowledge of the Lithobiomorpha (Chilopoda) in the Palestinian region.
Based on the material of fam. Henicopidae and Lithobiidae (Lithobiomorpha) collected in Israel during the year 1990 by S. NEGREA and others, the authors present some new systematical, ecological and zoogeographical data concerning the species belonging to the genera *Lamyctes*, *Eupolybothrus* and *Monotarsobius*. A new species, *Monotarsobius teldanensis* n. sp. is described. The paper also contains general remarks on the fauna of Lithobiomorpha from the Palestinian region.

INTRODUCTION

La région palestinienne peut être délimitée par la côte méditerranéenne à l'Ouest, la Péninsule Arabique à l'Est, le Mont Hermon au Nord et le golfe Elat-Aqabah au Sud. Les chilopodes de cette région géographique sont encore insuffisamment connus. Les premières contributions ont été publiées dans la période 1893-1934, particulièrement par ATTEMS, PORAT, SILVESTRI et VERHOEFF, synthétisées ultérieurement par BODENHEIMER (1937). Selon ce dernier auteur, cinq espèces de lithobiomorphes ont été signalées jusqu'en 1937 dans la région palestinienne : *Archilithobius carinatus* Koch (=*macrops* Karsch), *Lithobius parvicornis* Porat, *Lithobius vosseleri* Verhoeff, *Monotarsobius barbipes* Porat et *Polybothrus fasciatus* Newport. La systématique actuelle ne reconnaît parmi elles que quatre espèces et une sous-espèce : 1) *Lithobius carinatus* L. Koch 1862 - (syn. *Lithobius macrops* Karsch, 1888); 2) *Lithobius parvicornis* (Porat, 1893) ; 3) *Hessebius barbipes* (Porat, 1893) - (syn. *Lithobius vosseleri* Verhoeff,1901) ; 4) *Eupolybothrus litoralis* (L. Koch, 1867) - (syn. *Lithobius fasciatus* sensu Porat, 1893 non *Eupolybothrus fasciatus* (Newport, 1844) et *Polybothrus fasciatus graecus*

NEGREA, S. & MATIC, Z., 1996. — Contribution à la connaissance des lithobiomorphes (Chilopoda) de la région palestinienne. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 225-233. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

var. *fasciatograecus* Verhoeff, 1901. C'est ZAPPAROLI (1991) qui a apporté la plus récente et importante contribution à la connaissance des chilopodes de cette aire de grand intérêt biogéographique. Il a ajouté les 5 espèces supplémentaires suivantes : *Harpolithobius halophilus* Verhoeff, 1941, *Lithobius viriatus* Sseliwanoff, 1879, *Lithobius erythrocephalus* C. L. Koch, 1847, *Monotarsobius crassipes* L. Koch, 1862 et *Monotarsobius bolognai* Zapparoli, 1991.

Dans le cadre des programmes dirigés à Jérusalem par le Professeur F. D. POR (cf. POR, 1975 ; POR *et al.*, 1995), l'un de nous (S. N) a récolté, en mai-juin 1990, des chilopodes d'Israël et il lui a été confié pour étude le matériel conservé dans les collections zoologiques des Universités de Tel Aviv et de Jérusalem, pour la rédaction de sa contribution dans le volume de la série *Fauna Palaestina*. Parmi ce matériel, seuls les lithobiomorphes Henicopidae et Lithobiidae appartenant aux genres *Lamyctes*, *Eupolybothrus* et *Monotarsobius*, ont été étudiés à ce jour ; les résultats sont publiés dans ce travail. Les genres *Hessebius* et *Lithobius* s. str. plus riches en espèces, feront l'objet d'autres publications (NEGREA & MATIC, 1995).

LES ESPÈCES IDENTIFIÉES

Les données pour chaque espèce comprendront les synonymies, le matériel examiné, la description des espèces ou des populations nouvelles, la redescription des espèces insuffisamment décrites, les notes morphologiques complémentaires des espèces insuffisamment connues et les remarques éventuelles.

Les différentes collections sont désignées par les abréviations suivantes : HUJ = Hebrew University of Jerusalem, Zoological Museum; UTA = Tel-Aviv University, Zoological Museum.

Fam. HENICOPIDAE Pocock, 1901

Lamyctes coeculus (Brölemann, 1889) (Figs. 1-3)

Synonymies: *Lithobius coeculus* Brölemann, 1889 ; *Lamyctes coeculus* Attems, 1908; *Lamyctes coeculus* Silvestri,1909.

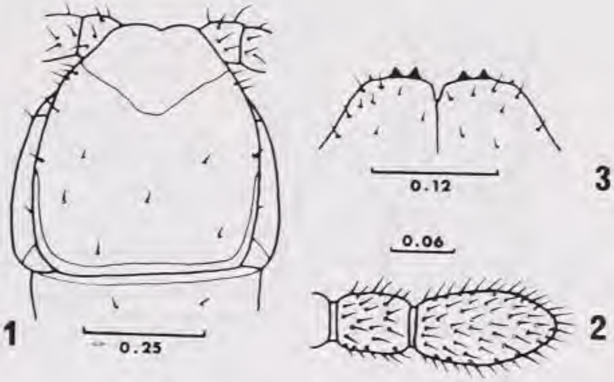
Matériel étudié: 4 ♀♀ *maturus senior*, plantation irriguée de peupliers près du Kibbutz Gonen (Vallée de Hula, Galilée supérieure, alt. +67 m), sol alluvial couvert de feuilles mortes et de débris de végétaux, température du sol 28°C, 28.5.1990, leg. S. NEGREA et C. DIMENTMAN, HUJ ; 1 ♀ *maturus senior*, plantation irriguée de pamplemousse près du Kibbutz En Gedi (Oasis En Gedi sur le bord ouest de la Mer Morte, alt.-370 m), sol mélangé, débris végétaux et fragments calcaires, température du sol 26°C, 2.6.1990, leg, S. NEGREA, HUJ.

Redescription. La description de BROLEMANN (1930) étant très sommaire, nous présentons les caractères des cinq femelles examinées. Longueur des adultes : 4,3 - 5,2 mm. Coloration jaune-pâle, avec les extrémités (capsule céphalique, forcipules et tergites 8-16) intensément orangées. Corps à bords parallèles, élancés. Téguments luisants, finement réticulés ; pilosité plus dense sur les tergites 13-16. Une paire de stigmates sur le premier segment. Tête atténuée en avant, plus longue que large (Fig.1) ; sillon frontal évident ; le bord caudal rectiligne. Antennes très courtes, pileuses, formées de 24+24 ou 24+18 articles courts, dont le dernier est presque égal aux deux précédents, en forme de massue (Fig. 2). Pas d'ocelles. Organe de Tömösvary indistinct. Bord rostral du coxosternum forcipulaire (Fig. 3) proéminent portant 2+2 dents plus ou moins noires de dimension moyenne et peu aiguisées ; 1+1 dents rudimentaires externes, écartées des autres, à l'aspect de courte épine, placées exactement dans la position des porodontes. NEGREA (1989) a nommé ces denticules "pseudoporodontes" et non "porodontes", comme les désigne ZALESSKAJA (1978). Des soies longues près du bord rostral. Tergites à angles arrondis ou droits ; bord caudal quasi droit ou un peu échancré pour les tergites 8, 10, 12, 14 et 16. Pores coxaux ronds et relativement grands, au nombre de 1 à 2 pour chaque hanche (1, 2, 2, 2 ou 2, 2, 2, 2). Pattes totalement dépourvues d'épines mais avec un prolongement acuminé à l'extrémité du tibia des P1 à P11, sur la face antérieure. Pattes 1-12 avec tarse soudé au métatarse ; il est indépendant seulement des P13 aux P15. La patte 15 est plus longue que la

Source : MNHN, Paris

patte 14, mais ne dépasse pas la longueur de l'antenne. Griffe apicale des pattes 1-15 flanquée de chaque côté d'une griffe accessoire plus petite. Appendices génitaux des femelles armés de 2+2 éperons coniques, relativement longs et pointus. La griffe est nettement délimitée à la base, courte, très arquée et sans dentelures latérales. Pas d'épine dorsale sur les trois articles du gonopode.

Remarques. Selon BROLEMANN (1930) il s'agit d'une "espèce exotique (Australie) importée, décrite des serres de Lombardie et également acclimatée dans celles du Muséum National d'Histoire Naturelle de Paris". La répartition de *L. coeculus* reste encore peu connue et discontinue. ENGHOFF (1975) indique Australie, Hawaii, Mexique, Tanzanie et des serres d'Europe (Danemark, Finlande, France, Italie et Suède). D'après NEGREA (1977), à Cuba celle-ci peut être considérée comme une forme édaphophile, les ♂♂ et ♀♀ étant plus fréquemment rencontrés dans le sol des forêts et sous les pierres plutôt que dans la litière (100-750 m alt.) ; elle a été trouvée avec *Lamyctes fulvicornis* de manière exceptionnelle. Il s'agit d'un genre et d'une espèce nouveaux pour la région palestinienne, rencontrés par l'un des auteurs seulement dans les plantations (donc probablement importés!) et représentés uniquement par des femelles (populations parthénogénétiques?).



FIGS. 1-3. — *Lamyctes coeculus* (Brölemann), ♀ : 1, Tête ; 2, Derniers articles de l'antenne ; 3, Bord rostral du coxosternum forcipulaire (mesures en mm) (orig. S. NEGREA).

FIGS 1-3. — Lamyctes coeculus *(Brölemann), ♀ : 1, Head; 2, Last antennal articles; 3, Rostral edge of the forcipular coxosternum (in mm) (after S. NEGREA).*

Fam. LITHOBIIDAE Newport 1844

Eupolybothrus (Eupolybothrus) litoralis (L. Koch, 1867) (Figs. 4-12)

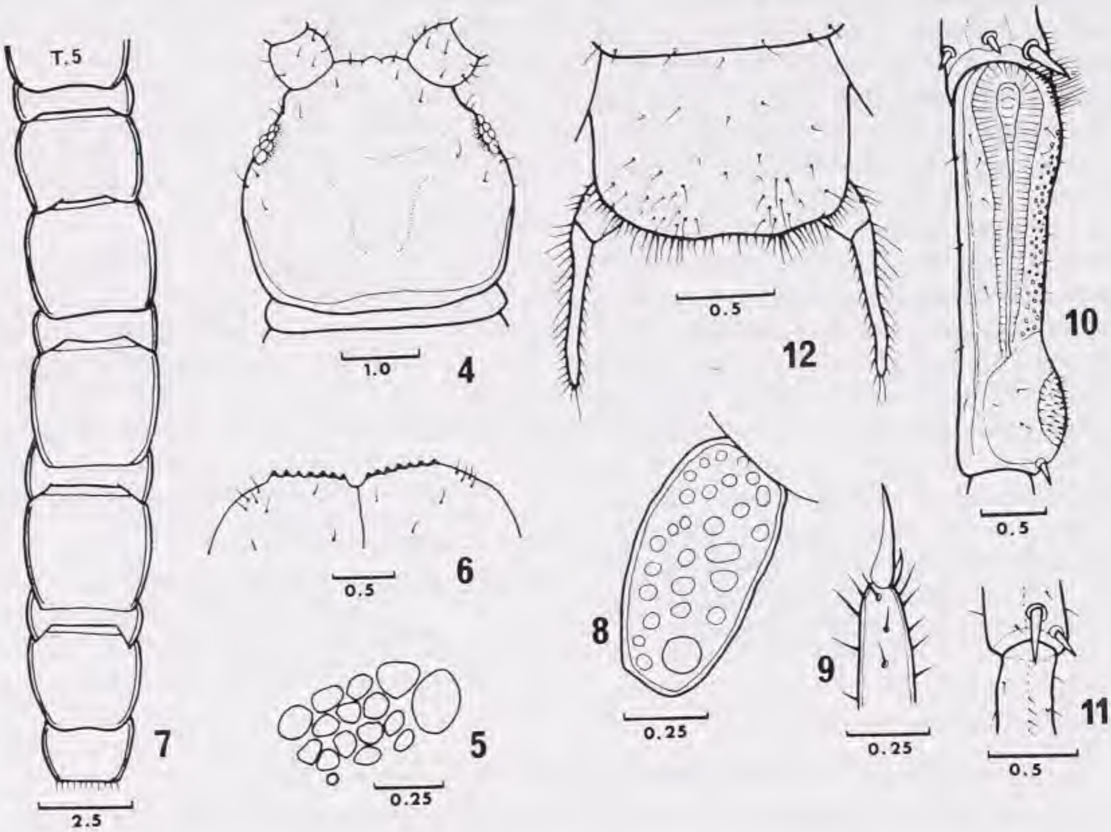
Synonymies : *Lithobius litoralis* L. Koch, 1867 (*nec* Muralewitsch, 1906); ? *Polybothrus fasciatus* Porat, 1993 (citée pour la localité Ain, Couffin); ? *Lithobius (Polybothrus) fasciatus graecus* var. *fasciatograecus* Verhoeff, 1901 (citée par VERHOEFF, 1925, des environs de Jaffa et du lac Tibériade = Kinneret) ; *Lithobius praecursor* Attems, 1902 (*nec Lithobius ankarensis praecursor* Verhoeff, 1943, décrit de Beyrouth); *Eupolybothrus litoralis* Eason, 1970 (redescription d'après l'holotype et les paratypes); *Eupolybothrus litoralis* Zapparoli, 1991 (citée des localités : Mont Hermon et Irbid).

Matériel étudié : 1 ♂ *maturus senior*, Nahal Bezet (= Wadi Qarzkara, Galilée supérieure), 8.4.1950, UTA; 1 ♂ *maturus senior*, Zikhron Ya'aqov (Monts Carmel), 21.1.1946, UTA.

Description de la population palestinienne. Étant donné que EASON (1970) a publié une redescription de cette espèce en utilisant la série type de la Grèce et que la population palestinienne n'a pas encore été décrite, il paraît utile de présenter les caractères des deux mâles examinés. Longueur : 30-32 mm. Coloration jaune-marron ; pattes et antennes presque jaunes. Tête (Fig. 4) plus large que longue. Antennes très longues, dépassant la moitié du corps, formées de 46 à 53 articles plus ou moins allongés. Ocelles (Fig. 5) de 14 à 16, en quatre rangées subrectilignes (1+4, 4, 4, 3 ; 1+4, 4, 4, 2). Organe de Tömösvary rond et très petit, situé tout près des ocelles. Coxosternum forcipulaire court; bord rostral (Fig. 6) très large, rectiligne, à échancrure médiane petite, armé de 7+7 dents petites ; pas d'épines externes (porodontes) spiniformes, mais des soies habituelles. Angles des tergites 1, 3, 5 arrondis ; ceux

Source : MNHN, Paris

des tergites 2, 4, 8, 10, 12, 14 presque droits avec le bord caudal plus ou moins échancré ; des prolongements aux tergites 6 et 7 (courts, larges et émoussés) et aux tergites 9, 11 et 13 (triangulaires, aigus) ; tergite terminal à angles faiblement arrondis et à bord caudal peu ou non échancré, portant de nombreuses soies (Fig. 7). Pores coxaux (Fig. 8) nombreux (de 23 à 32), ronds ou non, de dimensions variables, irrégulièrement disposés, dont l'un distal, relativement isolé et bien dessiné, toujours plus grand que les autres.



FIGS. 4-12. — *Eupolybothrus litoralis* (L. Koch), ♂ : 4, Tête; 5, Ocelles et organe de Tomösvary ; 6, Bord rostral du coxosternum forcipulaire ; 7, Tergites ; 8, Hanche droite de la P14 ; 9, Griffes apicales de la P15 (droite), vue dorsale ; 10, Fémur de la P15 (gauche), vue dorsale-interne ; 11, Articulation tarso-métatarsienne de la P14 (gauche), vue ventrale-interne ; 12, Sternite génital et appendices génitaux du mâle (mesures en mm) (orig. S. NEGREA).

FIGS 4-12. — Eupolybothrus litoralis *(L. Koch), ♂ : 4, Head; 5, Ocellae and Tomösvary organ; 6, Rostral edge of the forcipular coxosternum; 7, Tergites; 8, Right coxa of the P14; 9, Apical claws of the P15 (right), dorsal view; 10, Femur of the P15 (left), dorsal-internal view; 11, Tarso-metatarsial joint of the P14 (left), ventrale-internal view; 12, Genital sternite and genital appendix of the male (in mm) (from S. NEGREA).*

Les pattes 14 et 15 sont très longues (spécialement les P15 qui dépassent de beaucoup la moitié du corps) et relativement grêles. Pas d'épines coxolatérales. Griffe apicale secondaire interne des P15 dépassant le 1/3 de la principale (Fig. 9). Les pores glandulaires des P15 sont concentrés sur la face interne des fémur, tibia, tarse et métatarse. La pilosité du métatarse des P15 s'étend en longueur jusqu'aux 3/4 du diamètre de cet article. La série de soies ("seriate setae") du métatarse des P15 est absente. La fossette dorso-basale du fémur des P15 du mâle est grande et profonde ; le sillon interne qui la prolonge atteint ou non le bord de la nodosité dorso-distale interne ; cette nodosité, assez proéminente et toujours uniformément arrondie, porte une

Source : MNHN, Paris

aire centrale ovale relativement petite composée de pores glandulaires et de nombreuses soies fines et très courtes ; le sillon externe est très mince et long ; le fémur présente de même une touffe proximale de longues soies (Fig. 10). Les soies et les épines de la face ventrale-interne de l'articulation tarso-métatarsienne des P14 sont représentées Figure 11.

Spinulation des pattes (ventrale/dorsale)

P	H	tr	P	F	T	/	H	tr	P	F	T
1	-	-	*a*mp	amp	am-	/	-	-	amp	a--	a--
2-13	-	-	amp	amp	am-	/	-	-	amp	a-p	a-p
14	-	m	amp	amp	am-	/	a	-	amp	*a*-p	--p
15	-	m	amp	am-	-m-	/	a	-	amp	--p	---

Appendices génitaux ♂ (Fig. 12) biarticulés, longs, grêles et pileux ; bord rostral du sternite génital à échancrure médiane petite et soies marginales nombreuses.

Remarques. Cette espèce, nord-méditerranéenne et orientale, est connue avec certitude de la Grèce (y compris les îles de la Mer Egée - d'où elle a été décrite par L. KOCH), du sud-ouest de la Turquie, de Crète, Syrie, Liban, Jordanie et Israël. Nous ajoutons ici pour Israël deux stations nouvelles, l'une en Galilée supérieure (Nahal Bezet) et l'autre au Mont Carmel (Zikhron Ya'aqov).

Le matériel d'Israël a été comparé à des exemplaires de l'île Kassos (Grèce) empruntés par Marzio ZAPPAROLI et à la redescription de cette espèce faite par EASON (1970) d'après la série type des îles égéennes de Tinos et de Rhodes (Grèce). Les différences minimes constatées peuvent être considérées comme des variations individuelles qui caractérisent les populations palestiniennes. Ces différences sont les suivantes : longueur du mâle "*maturus*" d'Israël : 30-32 mm (matériel de Kassos : 30-31 mm ; matériel de Tinos et de Rhodes : 28-38 mm) ; ocelles : 14-16 en 4 rangées (12-14 en 3-4 rangées ; 16-18 en 4 rangées) ; bord rostral : 7+7 petites dents (7+7 ou 8+8 ; 8+8) ; pas de porodontes (idem; "lateral spines peg-like") ; pores coxaux : 23-32 irrégulièrement disposés (18-27 irrégulièrement disposés ; 30-55 en 4-5 rangées) ; un pore coxal distal plus grand et isolé (idem ; pas de mention) ; sillon externe du fémur des P15 long et mince, allant jusqu'à l'extrémité apicale de cet article (idem; "finer, extending to the margin of the pore-free area") ; nodosité dorso-distale interne du fémur des P15 toujours uniformément arrondie et assez proéminente, portant une aire centrale ovale de pores et de soies fines (idem ; "is barely swollen" avec l'aire centrale circulaire-ovale, sans soies!) ; épines de la P14 : DaT absente (présente ; présente) ; épines de la P15 : VpF, VaT et DpT absentes (VpF et DpT absentes ; VpF, VaT et DpT présentes).

Eupolybothrus litoralis est à rapprocher de *E. fasciatus* (Newport, 1844) connue avec certitude de Florence et de Naples (terra typica - voir EASON, 1970 et MINELLI & ZAPPAROLI, 1992), mais certains caractères séparent les deux espèces. Il s'agit surtout de : "seriate setae" du métatarse des P15 (*E. litoralis* : absente; *E. fasciatus* : présente), sillon externe du fémur des P15(présent ; absent) ; touffe proximale du fémur des P15 avec (des soies fine et longues ; des soies grossières et plus courtes) ; nodosité dorso-distale-interne du fémur des P15 (uniformément arrondie et relativement proéminente ; non-uniformément arrondie à cause de l'aire centrale ovale et mamillaire et fortement proéminente).

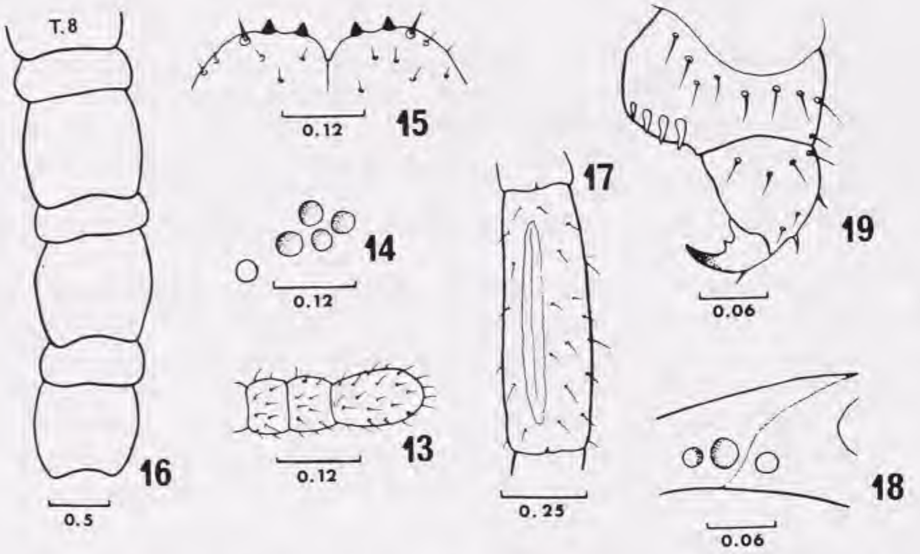
Monotarsobius teldanensis n. sp. (Figs. 13-17)

Matériel étudié : 1 ♂ *maturus senior* (holotype), réserve naturelle du bassin supérieur de la rivière Tel Dan (Galilée supérieure, alt. +190 m), sol calcaire de la forêt couvert de feuilles mortes, débris végétaux, bois pourri et pierres, température du sol 19,5 °C, 28.5.1990, leg. S. NEGREA, HUJ (lieu de conservation de l'holotype).

Derivatio nominis : du nom Tel Dan (terra typica).

Source : MNHN, Paris

Description de l'holotype (♂) : Longueur : 11,2 mm. Coloration jaune-paille. Téguments unis, brillants. Tête un peu plus large que longue, sans ponctuations distinctes, à bord caudal presque rectiligne et à bourrelet étroit et sans sinuosités. Antennes très courtes, de 20 articles, dont le dernier est environ le double du précédent (Fig. 13). Ocelles : 1+3 - pratiquement de la même dimension, disposés en croix (Fig. 14). Organe de Tömösvary plus petit qu'un ocelle. Coxosternum forcipulaire à bord rostral large, divisé par une encoche profonde et armé de 2+2 dents robustes, relativement rapprochées ; 1+1 porodontes spiniformes épais et longs (Fig. 15). Tous les tergites ont les angles arrondis et le bord caudal droit ou plus ou moins échancré ; pas de prolongements triangulaires postérieurs (Fig. 16). Pores coxaux : 3, 3, 3, 3 - petits et ronds.



FIGS. 13-17. — *Monotarsobius teldanensis* n. sp., ♂ : 13, Derniers articles de l'antenne ; 14, Ocelles et organe de Tomösvary ; 15, Bord rostral du coxosternum forcipulaire ; 16, Tergites ; 17, Fémur de la P.15 (gauche), vue dorsale (mesures en mm) (orig. S. NEGREA).

FIGS 13-17. — Monotarsobius teldanensis *n. sp., ♂ : 13, Last antennal articles; 14, Ocellae and Tomösvary organ; 15, Rostral edge of the forcipular coxosternum; 16, Tergites; 17, Femur of the P15 (left), dorsal view (in mm) (from S. NEGREA).*

FIGS. 18-19. — *Monotarsobius bolognai* Zapparoli, ♀ : 18, Appendice génital (gauche) ; 19, Ocelles et organe de Tomösvary (mesures en mm) (orig. S. NEGREA).

FIGS 18-19. — Monotarsobius bolognai *Zapparoli, ♀ : 18, Genital appendix (left); 19, Ocellae and Tomösvary organ (in mm) (from. S. NEGREA).*

L'articulation tarso-métatarsienne des P1 - P12 absente, celle de la P13 peu distincte et celles des P14 et P15 distinctes et fonctionnelles. Les deux dernières pattes plus épaisses que les autres, ayant leur face interne criblée de pores. Pas d'épines coxolatérales. Griffe apicale secondaire des P15 absente. Le fémur des P15 à sillon dorsal peu profond (Fig. 17). Spinulation des pattes (ventrale/dorsale) :

P	**H**	**tr**	**P**	**F**	**T**	/	**H**	**tr**	**P**	**F**	**T**
1	-	-	---	am-	-m-	/	-	-	--p	a-p	a-p
2-6	-	-	-m-	am-	-m-	/	-	-	--p	a-p	a-p
7-10	-	-	-mp	am-	am-	/	-	-	a-p	a-p	a-p
11	-	-	-mp	amp	am-	/	-	-	amp	a-p	a-p
12	-	-	-mp	amp	am-	/	-	-	amp	--p	---
13	-	m	-mp	amp	am-	/	-	-	-mp	--p	---
14	-	m	amp	-mp	---	/	-	-	-mp	---	---
15	-	m	amp	-mp	---	/	a	-	-mp	---	---

Source : MNHN, Paris

Le premier sternite génital avec 5+6 soies ; le deuxième arrondi et pourvu d'une soie apicale.

Diagnose. 11,2 mm de longueur ; 20 articles antennaires, 1+3 ocelles disposés en croix ; 2+2 dents au bord rostral du coxosternum ; 1+1 porodontes épais et longs ; 3, 3, 3, 3 pores coxaux ; épines coxolatérales absentes ; griffe de la P15 simple ; fémur de la P15 du mâle avec un sillon ; spinulation assez riche pour un *Monotarsobius* (voir au-dessus).

Diagnose comparative. *Monotarsobius teldanensis* n. sp. est connu uniquement de la localité type. Il se rapproche de *M. schizus* décrit par CHAMBERLIN en 1952 de Turquie (uniquement d'après le mâle) mais les caractères suivants distinguent les deux espèces : nombre des ocelles (1+3 au lieu de 1+3, 2) ; encoche du bord rostral (en forme de V et non de U) ; forme de porodonte (spiniforme, épais et long - et non spiniforme, court et grêle) ; nombre des pores coxaux (3, 3, 3, 3, au lieu de 2, 2, 2, 2) ; petit lobe distal du tibia des P15 absent chez *M. t.* et présent chez *M. s.*) ; spinulation (P1 : 00021/00122 et non 00000/00001 ; P14 : 01320/00200 et non 01321/00200 ; P15 : 01320/10200 et non 01320/10210). Une comparaison plus approfondie entre *M. teldanensis* et *M. schizus* est toutefois difficile à établir du fait que Chamberlin a décrit incomplètement son espèce, sans aucune illustration.

Monotarsobius bolognai Zapparoli, 1991 (Figs. 18-19)

Matériel étudié : 1 ♀ *maturus senior*, réserve naturelle Shemurat haMasreq (Monts de Judée, alt. +600 m), sol calcaire de la forêt couvert de feuilles mortes et de bois pourri, température du sol 16°C, 12.5.1990, leg. S. NEGREA, HUJ.

Notes morphologiques : la femelle de 7,5 mm de longueur correspond à la diagnose et à la description (spinulation incluse) de ZAPPAROLI (1991). On observe cependant quelques différences : organe de Tömösvary de dimension intermédiaire entre celle de l'ocelle postérieur et celle de l'unique ocelle antérieur (Fig. 18), articulation tarso-métatarsienne des P1 - 12 absente, trace d'articulation non fonctionnelle aux P12 et P13, gonopode à 4+4 éperons et à griffe étroite et pointue, pourvue d'une dentelure externe et d'une épine dorsale grêle, deux épines dorsales sur le second article du gonopode (Fig. 19).

Remarques : *M. bolognai* est connue seulement de trois stations de la région palestinienne, relativement anthropisées et à substrat calcaire : Wadi Kafrein (versant oriental de la dépression de la Mer Morte), Wadi Tajiba et Jaar na Nabi (Jérusalem). Une nouvelle s'ajoute aux deux premières, Shemurat haMasreq, qui est une forêt de *Quercus callyprinos*, *Pistacia*, *Arbutus* et *Pinus* non irriguée, installée sur roche calcaire, près de la localité Bet Meyr.

Monotarsobius crassipes L. Koch, 1862

Matériel étudié : 1 ♀ *maturus senior* (11 mm de longueur), 2 ♂♂ *praematurus* (6,5-7,5mm) et 3 ♂♂ *immaturus* (4,5-5,8 mm), plantation irriguée de peupliers près de kibbutz Gonen (Vallée de Hula, Galilée supérieure, alt. +67 m), sol alluvial couvert de feuilles mortes et de débris végétaux, température du sol 28°C, 28.5.1990, leg. S. NEGREA, A. NEGREA et I. CAPUSE, HUJ ; 2 ♂♂ *pseudomaturus* (7,5-8,2 mm), 1 ♂ *praematurus* (6,4 mm) et 1 ♂ *immaturus* (5,3 mm), grotte Me'arat Sharakh (Vallée Nahal Sharakh, Galilée supérieure, alt. +300 m), sur le plancher calcaire avec sol argileux et déchets abandonnés par les visiteurs de la grotte, 6.6.1990, leg. V. DECU et C. DIMENTMAN, HUJ.

Notes morphologiques : le ♂ et la seule ♀ examinés correspondent aux caractéristiques signalées par EASON (1964) dans sa description et ses dessins.

Remarques : espèce paléarctique occidentale (Europe, Afrique du Nord, Proche et Moyen Orient et Asie Centrale). Dans la région palestinienne, l'espèce est connue du Liban (Becherré), de la Jordanie (Petra) et d'Israël (Allone Abba, Segev et Basmat Tivon) (ZAPPAROLI, 1991). A ces stations, nous en ajoutons deux d'Israël : une grotte et une plantation de peupliers de la Galilée.

Source : MNHN, Paris

CONCLUSIONS

L'étude du matériel ci-dessus révèle la présence de cinq espèces : *Lamyctes coeculus* (Brölemann, 1889), genre et espèce nouveaux pour la région palestinienne ; *Monotarsobius teldanensis*, espèce nouvelle pour la science ; *Eupolybothrus litoralis* (L. Koch, 1867), *Monotarsobius bolognai* Zapparoli, 1991, et *M. crassipes* L. Koch 1862, ces trois derniers ont déjà été citées de la zone d'étude mais récoltées dans des stations nouvelles. Ainsi, le nombre des lithobiomorphes connus de la région palestinienne est passé de 9 à 11 espèces. Du point de vue zoogéographique, celles-ci peuvent être rattachées à différentes catégories. Le genre *Lamyctes* a un seul représentant, *L. coeculus*, élément holotropical à répartition discontinue, qui fut sommairement décrit par BRÖLEMANN (1889). Il est redécrit d'après des échantillons d'Israël, peut-être issus de femelles parthénogénétiques (?) importées. Le genre *Eupolybothrus* est également représenté par une seule espèce, *E. litoralis* (L. Koch), qui est, d'après ZAPPAROLI (1991), un élément nord-méditerranéen et oriental. Le genre *Hessebius* a deux représentants : *H. barbipes* (Porat) qui est une espèce est-méditerranéenne touranienne, très fréquente dans la région palestinienne et *H. halophilus* Verhoeff dont la géonémie est nord-méditerranéenne (ZAPPAROLI, 1991). Le genre *Monotarsobius* est représenté par trois espèces, toutes récoltées par les auteurs en Israël : *M. crassipes* L. Koch, espèce paléarctique occidentale qui a été capturée dans une grotte et dans une plantation de peupliers (nombreux adultes et juvéniles) ; *M. bolognai* Zapparoli, endémique de la région palestinienne (cantonnée particulièrement dans la zone de la Mer Morte) et apparentée à des espèces sibériennes (ZAPPAROLI, 1991) ; *M. teldanensis* n. sp., probablement endémique dans cette région et apparentée à *M. schizus* Chamberlin, connue de la Turquie. Enfin, le genre *Lithobius* s. str., qui sera étudié dans un prochain travail, a, pour le moment, quatre représentants : deux espèces nord-méditerranéennes orientales (*L. carinatus* L. Koch et *L. parvicornis* Porat), une sud-est européo-anatolico-caucasienne (*L. viriatus* Sseliwanoff) et une paléarctique occidentale (*L. erythrocephalus* L. Koch).

La faune des Lithobiomorphes de la région palestinienne se révèle très intéressante et remarquable par les espèces endémiques et d'origine méditerranéenne qui constituent la majorité de la faune. La diversité spécifique n'est pas élevée. Les stations occupées par des chilopodes corespondent aux biotopes naturels protégés dans des réserves naturelles (par exemple Tel Dan et Shemurat haMasreq) ou à ceux des vallées boisées traversées par des rivières (par exemple Nahal Sharakh). Dans les biotopes anthropisés (telles les plantations irriguées de Gonen et En Gedi) la diversité est moindre, mais la densité des individus plus grande.

REMERCIEMENTS

Nous adressons nos vifs remerciements à M. le Professeur F. D. POR (Jérusalem) pour son aimable invitation à étudier sur place les chilopodes et pour l'aide qu'il nous a apportée en Israël, à M. le Docteur M. ZAPPAROLI (Viterbo) pour le matériel de comparaison d'*Eupolybothrus litoralis* et *E. fasciatus* qu'il nous a confié, ainsi que pour son aide bibliographique et ses informations précieuses.

RÉFÉRENCES

BODENHEIMER, F. S., 1937. — Prodomus faunae Palestinae. *Mém. Inst. Egypte*, **33** : 233-234.

BRÖLEMANN, H. W., 1889. — Contributions à la faune myriapodologique méditerranéenne. Trois espèces nouvelles. *Ann. Soc. Linn. Lyon* : 5-16.

BROLEMANN, H. W., 1930. — *Eléments d'une faune des Myriapodes de France. Chilopodes.* [*Faune de France*, **25**]. Paris, P. Lechevalier, 1-405

CHAMBERLIN, R. V., 1952. — On the Chilopoda of Turkey. *Rev. Fac. Sci. Univ. Istanbul, ser. B. Sci. Nat.*, **17** : 183-258.

EASON, E. H., 1964. — *Centipedes of the British isles*. London, F. Warne & Co, 294 pp.

EASON, E. H., 1970. — A redescription of the species of *Eupolybothrus* Verhoeff *s. str.* preserved in the British Museum (Chilopoda, Lithobiomorpha). *Bull. British Mus. London*, **19** : 289-310.

Source : MNHN, Paris

ENGHOFF, H., 1975. — Notes on *Lamyctes coeculus* (Brölemann) a cosmopolitic parthenogenetic centipede (Chilopoda : Henicopidae). *Ent. Scand.*, **6** : 45-46.

MINELLI, A. & ZAPPAROLI, M., 1992. — Considerazioni faunistiche e zoogeografiche sui chilopodi delle alpi occidentali. *Biogeographia*, **16** : 211-243.

NEGREA, S., 1989. — Sur la présence de *Lamyctes fulvicornis* Meinert, 1868 (Chilopoda : Henicopidae) en Roumanie. *Misc. speol. Rom.* , **1** : 169-174.

NEGREA, S., 1977. — Considérations écologiques et biogéographiques sur les Chilopodes de Cuba. *Rés. Expéd. Biosp. Cubano-roumaines à Cuba*, **2** : 303-312.

NEGREA, S. & MATIC, Z., 1995. — Étude comparative de la variabilité de trois populations de *Hessebius barbipes* (Porat, 1893) (Chilopoda : Lithobiidae). *Soil Fauna of Israël*, **1** : 29-39.

POR, F. D., 1975. — An Outline of the Zoogeography of the Levant. *Zool. Scripta*, **4** : 5-20.

POR, F. D., DECU, V., NEGREA, S. & DIMENTMAN, C. 1995 — A survey of the edafic fauna of Israel. Results of a Romanian-Israeli joint collecting programme (May-June, 1990). *Soil Fauna of Israël*, **1** : 1-17.

PORAT, C. O., 1893 . — Myriapodes récoltés en Syrie par le Docteur Théodore Barrois. *Rev. Biol. Nord France*, **6** : 62-79.

VERHOEFF, K. W., 1925. — Mediterranean Chilopoden und Notiz zur Periodomorphose der Juliden. *Zool. Anz.*, **64** : 61-80.

ZALESSKAJA, N. T., 1978. — Opredeliteli mnogonojek kostyanok SSSR (Chilopoda, Lithobiomorpha). Moscou, Nauka, 211 pp.

ZAPPAROLI, M., 1991. — Note su alcune specie di Chilopodi della regione palestinese. *Fragm. Entomol.* , **23** : 15-33.

Source : MNHN, Paris

Source : MNHN, Paris

Check-List, Distribution and Habitat in Bulgarian Centipedes

***Georgi* RIBAROV**

Natural History Department of Regional Museum, 2 Dzaldeti Str., BG-8600 Jambol, Bulgaria

ABSTRACT

This preliminary survey of the Bulgarian centipede fauna is based on bibliographic data, collections and recent material examined by the author. The present check-list includes 26 species of Geophilomorpha, 5 species of Scolopendromorpha, 67 species of Lithobiomorpha and 1 species of Scutigeromorpha. Subspecies are not listed because of their uncertain status. The district and altitudinal distribution of the centipedes is shown in Table 1. 42% of all the species recorded in the country are Bulgarian or Balkan endemics. Most endemic species are known from Rhodopi Mts. (37%) and Strandza Mts. (35%). Some species (*Thracophilus bulgaricus* Verhoeff, *T. beroni* Matic & Darabantzu) show the connections between the Bulgarian (respectively Balkan) fauna with that of Asia Minor.

RÉSUMÉ

Les Chilopodes de Bulgarie : liste des espèces, répartition et habitat.

Cet inventaire préliminaire de la faune des chilopodes de Bulgarie est basé sur les données de la littérature, sur les collections existantes et sur du matériel récemment analysé par l'auteur. La liste des espèces inclut 26 Geophilomorpha, 5 Scolopendromorpha, 67 Lithobiomorpha et 1 Scutigeromorpha. Les sous-espèces ne sont pas prises en considération à cause du caractère trop incertain de leur statut. L'aire de répartition et la distribution verticale sont données par le Tableau 1. 42% de toutes les espèces répertoriées sont des endémiques de Bulgarie ou des Balkans. Le plus grand nombre d'espèces endémiques se trouve dans les Monts Rhodope (37%) et dans les Monts Strandza (35%). Certaines espèces (telles *Thracophilus bulgaricus* Verhoeff et *T. beroni* Matic & Darabantu) montrent l'existence de connexions entre la faune bulgare (et balkanique) et celle de l'Asie Mineure.

INTRODUCTION

The formation of the present day Bulgarian centipede fauna can be generally divided into three historical periods: Tertiary, Pleistocene and Postglacial (GRUEV, 1981). At the end of the Miocene and at the beginning of the Pliocene, the tropical and subtropical climate in South Europe and in the Balkan peninsula changed to more temperate conditions. At the same time Bulgaria fell under the influence of the Central European fauna from the north and Asiatic fauna from the north-east.

The second main period in the formation of the Bulgarian centipede fauna began during the Pleistocene, when North America, Europe and Siberia were covered with an ice belt. Under the influence of this cold spell, the climate changed in the Balkan peninsula (including Bulgaria).

RIBAROV, G., 1996. — Check-list, distribution and habitat in bulgarian centipedes. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 235-241. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

The glaciation enveloped the high Bulgarian Ryla and Pirin mountains. In the lower southern mountains: Strandza, Sakar and the eastern parts of the Rhodopi Mts., the influence of the cold spell was on a lesser scale. Many species of Chilopoda have found here more favourable conditions.

TAXONOMIC OBSERVATIONS

Contributions to the study of the centipedes (Chilopoda) of Bulgaria have been made by several authors (JURINICH, 1904; VERHOEFF, 1926-1928; FOLKMANOVA, 1936; MATIC, 1964-1973b; MATIC & DARABANTU, 1968; MATIC & GOLEMANSKY, 1964-1967c; NEGREA, 1965, 1971; KACZMAREK, 1969a, 1975; RIBAROV, 1984-1992). In 1936, FOLKMANOVA recorded the species *Scolopendra morsitans* (L.) from Strandza Mts., Southeastern Bulgaria. During the period 1980-1984, the present author collected numerous specimens of the genus *Scolopendra* in Southeastern Bulgaria and examined them. On the base of this and the examination of the collections of Chilopoda in the Natural History Museum, Sofia, RIBAROV (1984) considered that probably FOLKMANOVA (1936) has wrongly identified some specimens of *S. cingulata* Latreille as *S. morsitans* and in fact the last species does not occur in Bulgaria. On the other hand, RIBAROV (1989a) identified the subspecies *S. cingulata thracia* Verhoeff as a new synonym of *S. cingulata*. The lithobiomorphs *Eupolybothrus grossipes* (C. L. Koch) and *Lithobius borisi* (Verhoeff) were also removed from the Bulgarian faunal list (RIBAROV, 1989a). The first one as misidentified by JURINICH (1904) and the second as a new synonym of *Lithobius erythrocephalus* (C. L. Koch).

In the present paper, subspecies are not listed because of their uncertain status. There are some cases of different subspecies of the same species which reported from the same locality. Such are: *Cryptops anomalans anomalans* Newport and *C. a. schassburgensis* Verhoeff, *C. parisi parisi* Brolemann and *C. p. rhenanus* Verhoeff. The taxonomic status of the subspecies *Pachymerium ferrugineum insulanum* Verhoeff also needs an examination. The description of the specimens of *P. f. insulanum* Verhoeff, anounced by KACZMAREK (1969a) from the Bulgarian Black Sea coast show significant differences (more various than those peculiar for the subspecies level) with the nominate form *P. f. ferrugineum* C. L. Koch recorded in the same region (RIBAROV, 1984-1990).

ZOOGEOGRAPHICAL DISTRIBUTION AND HABITAT

To clarify the distribution of the centipedes and their habitat preferences, the Bulgarian territory is divided here into 7 regions, on the basis of climatic-geographic principles: 1 - Black Sea coast (BSC), 2 - North Bulgaria (NB), 3 - Thracean region (TR), 4 - Central mountains (CM), 5 - Southwestern region (SW), 6 - Ryla-Rhodopi region (RR) and 7 - Strandza Mts. (SM) (Fig.1). The check-list and distribution are presented in Table 1.

The western, higher and more humid parts of the Rhodopi Mts. were included in RR, but the eastern lower and more arid parts of the same Mts. remains in TR.

42% of all the centipedes established in the country are Bulgarian or Balkan endemics. Comparing the regions, the largest percentage of endemics is found in the Strandza Mts.(35%) and in Ryla-Rhodopi region (32%). Somewhat larger is the respective percentage in the Rhodopi Mts. which fall into neighbouring regions - RR and TR (Fig.1). Some of the Bulgarian endemic species: *Geophilus balcanicus* Kaczmarek, *Lithobius electron* Verhoeff, *L. glaciei* Verhoeff, *L. rylaicus* Verhoeff, *L. jurinici* Matic & Golemansky, are recorded only from the high parts of the mountains of the Ryla, Pirin, Stara Planina range and W-Rhodopi. Probably the above mentioned species belong to isolated communities of an older Euro-Siberian faunistic complex. On the other hand, in the East-Rhodopi, Sakar Mts. and Strandza Mts. (2/3 of the last extend south into Turkey), many thermophilic endemic species have evolved and survived. Such are: *Henia angelovi* Ribarov, *Lithobius maculipes* Folkmanova, *L. tiasnatensis* Matic, *L. thracicus*

Source : MNHN, Paris

Matic & Golemansky, *L. golemanskyi* Ribarov, *L. strandzanicus* Ribarov, *Harpolithobius folkmanovae* Kaczmarek.

FIG. 1. — Zoogeographical regions in Bulgaria. 1 - Black Sea coast (BSC), 2 - North Bulgaria (NB), 3 - Thracean region (TR), 4 - Central mountains (CM), 5 - Southwestern region (SW), 6 - Ryla-Rhodopi region (RR), 7 - Strandtza mountains (SM).

27% of all Bulgarian centipedes belong to European and Central European faunistic elements, but their percentage is not the same in the different regions. In North Bulgaria, these species are 40% and in the Central Mts. 35%. This percentage is smaller in the Strandza Mts.(32%) and in the Southwestern region (32%). The more thermophilic South European, South-East European and Central-South European faunal patterns established in Bulgaria are 14%; the Mediterranean -11%. The highest percentage of Mediterranean faunistic elements were recorded from the Black Sea coast (26%) and from the Southwestern region (20%). This is connected with the climatic influence and with the location of the two above mentioned regions in the path of Mediterranean migrants. The number of Mediterranean species occuring in the Strandza Mts. and in the Thracean region is also high. In spite of this, their percentage is respectively 16% and 14%, because of the numerous endemic species occurring in the same regions.

The thermophilic endemic species *Thracophilus bulgaricus* Verhoeff and *T. beroni* Matic & Darabantu seem to be good indicators of the connections between the Balkan and the Asia Minor fauna in Bulgaria. The endemics *T. cilicus* Attems and *T. pachypus* Verhoeff are representatives of the genus *Thracophilus* Verhoeff in Asia Minor according to ZAPPAROLI (1990).

Some of the thermophilic species distributed south of the Central Bulgarian mountains prefer more humid biotopes rich in vegetation: *Harpolithobius folkmanovae* Kaczmarek, *Lithobius beroni* Negrea, *Pleurolithobius jonicus* (Silvestri). Other taxa such as *Henia angelovi* Ribarov and *Lithobius peregrinus* Latzel occur in more arid and open sites.

Source : MNHN, Paris

TABLE 1. — Present knowledge of the centipede fauna (Chilopoda) of Bulgaria - Distribution according to the regions (BSC-Black Sea coast, NB - North Bulgaria, TR - Thracean region, CM-Central Mts., SW - Southwestern region, RR - Ryla-Rhodopi region, SM-Strandza Mts.) - Vertical distribution (V.D.) m a.s.l.; Zoogeographic distribution (Z.D.): en - Endemic, ben - Balkan endemic, il - Illiric, me - Mediterranean, eme - East Mediterranean, se - South European, see - South-East European, cse - Central-South European, e - European, ce - Central European, t-e-me - Turano-Euro-Mediterranean, e-a - Euro-Asiatic, co - Cosmopolitan.

Distribution Species	BSC	NB	TR	CM	SW	RR	SM	V. D.	Z.D.
GEOPHILOMORPHA									
Bothriogaster signata Attems, 1926				+				150	eme
Brachyschendyla varnensis Kaczmarek, 1968	+							100	en
Clinopodes flavidus C. L. Koch, 1847	+	+	+	+	+	+	+	0-2100	e-a
Dignathodon microcephalum (Lucas, 1846)	+		+	+				0- 700	me
Geophilus balcanicus Kaczmarek, 1972						+	+	1300-1400	en
G. electricus (L., 1758)	+							100	e
G. flavus (De Geer, 1783)	+		+	+	+		+	50-1000	e
G. linearis C. L. Koch, 1835			+	+	+	+	+	150-2500	e
G. proximus C. L. Koch, 1847			+	+				250- 600	e
G. rhodopensis Kaczmarek, 1970			+			+	+	150-1800	en
G. strictus Latzel, 1880					+			400- 500	ben
Henia angelovi Ribarov, 1987			+	+			+	150- 700	en
H. bicarinata (Meinert, 1870)				+	+			250- 600	me
H. illyrica (Meinert, 1870)	+	+	+	+	+	+	+	0-1600	il
Himantarium gabrielis (L., 1767)	+		+		+		+	0-1450	me
Pachymerium ferrugineum C. L. Koch, 1835	+		+	+		+	+	0-1100	t-e-me
P. flavum Folkmanova, 1949	+		+	+		+	+	0- 700	ce
Schendyla delicatula Kaczmarek, 1969	+							100	en
S. montana Attems, 1895			+	+				500-1300	cse
S. nemorensis (C. L. Koch, 1836)						+		550	e
S. walachica Verhoeff, 1900						+		600- 700	ben
Strigamia acuminata (Leach, 1815)			+	+		+		150-1000	e
S. crassipes (C. L. Koch, 1835)	+	+	+	+		+	+	0-2400	e
S. transsilvanica (Verhoeff, 1928)	+		+	+		+	+	0-1800	il
Thracophilus beroni Matic & Darabantu, 1973						+		450	en
T. bulgaricus Verhoeff, 1926			+			+		500- 800	see
SCOLOPENDROMORPHA									
Cryptops anomalans Newport, 1844	+		+	+	+	+	+	0-1800	e
C. croaticus Verhoeff, 1931	+	+	+	+	+	+	+	0-1800	eme
C. hortensis Leach, 1815	+			+	+	+		400-2000	e
C. parisi Brolemann, 1920		+	+	+	+	+	+	150-1850	e
Scolopendra cingulata Latreille, 1829	+	+	+		+		+	0-1100	me
LITHOBIOMORPHA									
Eupolybothrus andreevi Matic, 1964				+				600	en
E. fasciatus (Newport, 1845)	+	+	+	+	+	+	+	0-1100	se
E. ochraceus (Folkmanova, 1936)		+		+	+	+		100-2350	en
E. transsylvanicus (Latzel, 1882)			+	+	+	+		150-1800	see
E. tridentinus (Fanzago, 1874)	+		+	+	+	+	+	150-1600	cse
E. valkanovi Kaczmarek, 1973						+		600	en
Harpolithobius anodus (Latzel, 1880)		+		+	+	+		500-1650	see
H. aseni Kaczmarek, 1975						+		600	en

Source : MNHN, Paris

H. banaticus Matic, 1961						+		1450	ben
H. folkmanovae Kaczmarek, 1975	+		+		+		+	50- 500	en
H. hemusi Kaczmarek, 1975				+				900	en
H. radui Matic, 1955		+						250	ben
Lithobius aeruginosus L. Koch, 1862		+				+		300-1000	e
L. agilis C. L. Koch, 1847				+				300	e
L. audax Meinert, 1872			+					200- 300	see
L. balcanicus Matic, 1973						+		700- 800	en
L. beschkovi Matic & Golemansky, 1967				+				200- 400	en
L. bifidus Matic, 1973							+	150- 400	en
L. bulgaricus Verhoeff, 1925	+		+	+		+	+	0-1800	ben
L. burzenlandicus Verhoeff, 1931	+	+	+	+		+	+	0- 700	e
L. catascaphius Verhoeff, 1937						+		700	me
L. christovici Matic & Golemansky, 1964			+			+		400- 500	en
L. crassipes L. Koch, 1862	+	+	+	+	+	+	+	0-1100	e
L. curtipes C. L. Koch, 1847			+	+		+		400- 700	see
L. dalmaticus Latzel, 1880				+				800- 900	ben
L. diampolisi Ribarov, 1987			+				+	100- 400	en
L. dobrogicus Matic, 1962			+			+		200- 600	ben
L. duboscqui Brölemann, 1896	+			+		+		700-1900	eme
L. electron Verhoeff, 1927							+	2300	en
L. erythrocephalus C. L. Koch, 1847		+	+	+		+		100-2750	e
L. forficatus (L., 1758)	+	+	+	+	+	+	+	0-2500	e
L. glaciei Verhoeff, 1927				+				2200	en
L. golemanskyi Ribarov, 1987	+		+	+			+	150- 600	en
L. jurinici Matic & Golemansky, 1965						+		900-1900	en
L. lakatnicensis Verhoeff, 1926				+	+	+	+	250-1000	ben
L. lapidicola Meinert, 1872						+		700- 800	e
L. latro Meinert, 1872			+	+				150- 600	se
L. lucifugus L. Koch, 1862	+		+	+		+	+	0- 800	ce
L. maculipes Folkmanova, 1936							+	150- 400	en
L. microps Meinert, 1868		+	+					150- 400	e
L. mutabilis L. Koch, 1862				+		+		600- 800	ce
L. muticus C. L. Koch, 1847		+	+	+		+	+	100-1400	e
L. nigrifrons Latzel & Haase, 1880			+					100- 700	e
L. nigripalpis L. Koch, 1867	+		+	+		+	+	0-1800	me
L. oglednicus Ribarov, 1987				+			+	150- 400	en
L. parietum Verhoeff, 1899	+	+	+	+		+		100-2500	see
L. pelidnus Haase, 1880					+			300	e
L. peregrinus Latzel, 1880				+		+	+	150- 700	see
L. piceus L. Koch, 1862			+	+		+	+	200-1800	ce
L. popovi Matic, 1973				+				900	en
L. proximus Matic & Golemansky, 1967						+		600- 800	en
L. pusillus Latzel, 1880						+		700-1400	ce
L. pustulatus Matic, 1964	+						+	150- 400	ben
L. ruschovensis Matic, 1967						+		800	en
L. rylaicus Verhoeff, 1937						+		2500	cse
L. strandzanicus Ribarov, 1987							+	150- 400	en
L. beroni Negrea, 1965	+		+	+		+	+	150-1300	en
L. thracicus Matic & Golemansky, 1967			+					200	en
L. tiasnatensis Matic, 1973			+					300	en

Source : MNHN, Paris

L. totevi Kaczmarek, 1975				+				1000	en
L. trebinjanus Verhoeff, 1900				?		?		?	see
L. tricuspis Meinert, 1872			+					400- 500	ce
L. uniunguis Matic & Golemansky, 1967						+		200- 800	en
L. viriatus Sselivanoff, 1879			+	+	+	+		150-2100	see
L. vizicae Ribarov, 1987						+		150- 400	en
L. zelazovae Kaczmarek, 1975		+		+		+		250-1500	en
Pleurolithobius jonicus (Silvestri, 1896)	+		+	+		+	+	50- 600	eme
Lamyctes fulvicornis Meinert, 1868			+		+			150- 400	co
SCUTIGEROMORPHA									
Scutigera coleoptrata (L., 1758)	+	+	+	+		+	+	0- 800	me

CONCLUSION

The present knowledge of the centipede fauna of Bulgaria is obviously incomplete, for that reason, we suggest the present account has to be considered as a preliminary one. For instance, more data is necessary to complete the faunal list for North Bulgaria. Some species of *Lithobius* found in the Rhodopi Mts. are new for science and still in process of description. On an other hand, the taxonomic status of some subspecies and also species is of questionable validity.

From a zoogeographical point of view, the Bulgarian centipede fauna is very rich because of the geological history, the relief and the crossroad situation of the country. Here are distributed: Endemic, Central and South European, Holomediterranean and East Mediterranean, Euro-Asiatic and Balkan-Asia Minor zoogeographical faunistic elements.

The Bulgarian territory can be considered as a refuge for many species which survived the glacial periods. Moreover, the process of specification took place here in some geographically isolated populations. 42.4% of the species established in the country are Bulgarian or Balkan endemics. For the thermophilic species, the most important refuge from the Tertiary times up to now have been the mountains Strandza, Sakar and eastern parts of the Rhodopi Mts., for the Euro-Siberian patterns similarly the mountains of the Ryla, Pirin and Stara Planina range.

A considerable influence on the formation of the modern centipede fauna in Bulgaria was the migrations of the different faunistic elements. The most intensive pathways for the Mediterranean migrants from south to north across the Bulgarian territory have been the Black Sea coast and the valleys of the rivers Struma, Mesta, Toundztha, Maritsa and Arda.

The Central Bulgarian Mts. (Stara Planina range, Sredna Gora range, Vitosha) seemed to have played a role as a natural northern boundary for the thermophilic Mediterranean and South European centipedes such as *Dignathodon microcephalum* (Lucas), *Eupolybothrus tridentinus* (Fanzago) and *Pleurolithobius jonicus* (Silvestri), and one of the last locations for the Central European and Euro-Siberian elements, e. g. *Lithobius mutabilis* L. Koch which have migrated to the south.

REFERENCES

FOLKMANOVA, B., 1936. — Ueber einige von Dr. Jaroslav Storkan in Bulgarien gesammelte Chilopoden. *Izv. tsarsk. Prir. Inst.*, **9** : 92-97.

GRUEV, B., 1981. — *General biogeography*. Plovdiv : 205-209 (in Bulgarian).

JURINICH, S., 1904. — Contribution à la faune des Myriapodes en Bulgarie. *Sbor. Nar. Umotv.*, **20** : 1-44 (in Bulgarian).

KACZMAREK, J., 1969a. — Beiträge zur Kenntnis bulgarischer Chilopoda. Teil I. *Bull. Soc. Amis scien., Ser. D*, **9** : 263-277.

KACZMAREK, J., 1969b. — Beiträge zur Kenntnis bulgarischer Chilopoda. Teil II. *Bull. Soc. Amis scien., Ser. D*; **10** : 99-109.

KACZMAREK, J., 1970. — Beiträge zur Kenntnis bulgarischer Chilopoda. Teil III. *Bull. Soc. Amis scien., Ser. D*, **11** : 81-89.

Source : MNHN, Paris

KACZMAREK, J., 1972. — Beiträge zur Kenntnis bulgarischer Chilopoda. Teil IV. *Bull. Soc. Amis scien., Ser. D*, **12/13** : 261-264.

KACZMAREK, J., 1973. — Beiträge zur Kenntnis bulgarischer Chilopoda. Teil V. *Bull. Soc. Amis scien., Ser. D*, **14** : 181-192

KACZMAREK, J., 1975. — Beiträge zur Kenntnis bulgarischer Chilopoda. Teil VI. *Ann. Zool.*, **33** : 47-66.

MATIC, Z., 1964. — Description d'un nouveau Lithobiidae cavernicole de Bulgarie (Chilopoda). *Ann. Spel. Romania*, **XIX** : 507-510.

MATIC, Z., 1967. — Contribution à la connaissance des Chilopodes cavernicoles de Bulgarie. *Bull. Inst. Zool. (Bulgarie)*, **XXV** : 17-21.

MATIC, Z., 1973a. — *Lithobius balcanicus* n.sp. une nouvelle Lithobiidae (Chilopoda, Lithobiomorpha) de Bulgarie. *Bull. Inst. Zool. (Bulgarie)* , **XXXVIII** : 249-251.

MATIC, Z., 1973b. — Nouvelles contributions à la connaissance des Chilopodes cavernicoles de Bulgarie. *Bull. Inst. Zool. (Bulgarie)*, **XXXVIII** : 253-263.

MATIC, Z & GOLEMANSKY, V., 1964. — Contribution à la connaissance des Lithobiides (Chilopoda, Lithobiomorpha) en Bulgarie. *Ann. Univ. Sofia*, **LVII** : 99-106.

MATIC, Z & GOLEMANSKY, V., 1965. — Nouvelle contribution à la connaissance des Lithobiides (Chilopoda, Lithobiomorpha) en Bulgarie. *Ann. Univ. Sofia*, 58 : 13-25.

MATIC, Z & GOLEMANSKY, V., 1967a. — Recherches sur les espèces et l'écologie des Lithobiides (Chilopoda, Lithobiomorpha) en Bulgarie. *Bull. Inst. Zool. (Bulgarie)*, **XXIV** : 121-132.

MATIC, Z & GOLEMANSKY, V., 1967b. — Le sous-genre *Monotarsobius* (Chilopoda, Lithobiomorpha) en Bulgarie. *Bull. Inst. Zool. (Bulgarie)*, **XXIV** : 39-50.

MATIC, Z & GOLEMANSKY, V., 1967c. — Matériaux de la faune des Lithobiides (Chilopoda, Lithobiomorpha) en Bulgarie. *Bull. Inst. Zool. (Bulgarie)*, **XXV** : 17-21.

MATIC, Z. & DARABANTU, C., 1968. — Note critique sur quelques espèces du genre *Lithobius* (Chilopoda, Lithobiidae). *Bull. Inst. Zool. (Bulgarie)*, **XXVI** : 103-117.

NEGREA, S., 1965. — Contribution à l'étude des Lithobiidae (Chilopoda) en Bulgarie. *Fragm. Balcanica*, **V** : 91-104.

NEGREA, S., 1971. — *Lithobius* (*Monotarsobius*) *taschevi* Matic et Golemansky est un synonyme de *Lithobius* (*Monotarsobius*) *beroni* Negrea (Chilopoda, Lithobiomorpha). *Trav. Inst. Spéol. E. Racovitza*, **X** : 231-233.

RIBAROV, G., 1984. — Est-ce qu'on peut rencontrer en Bulgarie *Scolopendra morsitans* (L.)?. *Bull. Musées Bulg. SE*, **VII** : 273-276 (in Bulgarian).

RIBAROV, G., 1985. — Species list, ecology, distribution and importance of centipedes Lithobiomorpha (Chilopoda) from the mountains Strandza and Sakar. *Stran. Sakar. Sbor.*, **IV** : 279-287 (in Bulgarian).

RIBAROV, G., 1986a. — Contribution à la connaissance des Lithobiomorpha (Chilopoda) en Bulgarie Sud-est. *Trav. scien. Univ. Plovdiv*, **24** : 155-160 (in Bulgarian).

RIBAROV, G., 1987a. — Five new species Lithobiomorpha (Chilopoda) from Southeastern Bulgaria. *Acta Zool. Bulg.*, **34** : 45-52.

RIBAROV, G., 1987b. — *Henia angelovi* sp. n. (Chilopoda, Geophilidae) - Eine neue *Henia*-Art aus Südostbulgarien. *Acta Zool.*, **35** : 86-89.

RIBAROV, G., 1989a. — On some Chilopoda species (Myriapoda) published by S. Jurinich and K. Verhoeff. *Hist. nat. Bulg.*, **1** : 34-35.

RIBAROV, G., 1989b. — A contribution to the study of centipedes (Chilopoda) from the Sredna Gora Mountains range. *Trav. scien. univ. Plovdiv*, **27** : 165-184. (in Bulgarian).

RIBAROV, G., 1990. — Chilopoda new to the science or to the Bulgarian fauna. *In* : A. MINELLI, *Proc. 7th Int. Congr. Myriapodology*. Leiden, Brill : 429.

RIBAROV, G., 1992. — The distribution of the centipedes of the genera *Harpolithobius* and *Eupolybothrus* in Bulgaria. *Ber. nat.-med. Ver. Innsbruck*, **suppl. 10** : 361-372.

VERHOEFF, K. W., 1926. — Zwei neue Höhlen-Myriapoden aus Bulgarien. *Zool. Anz.*, **65** : 294-296.

VERHOEFF, K. W., 1927. — Zwei neue Geophilomorphen Gatungen aus Thracien und Mexico. *Zool. Anz.*, **69** : 97-105.

VERHOEFF, K. W., 1928. — Über Chilopoden aus Bulgarien gesammelt von Hernn Dr. I. Buresch. *Bull. Entom. Druz.*, **4** : 115-124.

ZAPPAROLI, M., 1990. — Distribution patterns and taxonomic problems of the centipede fauna in Anatolian peninsula. *In* : A. MINELLI, *Proc. 7th Int. Congr. Myriapodology*. Leiden, Brill : 51-59.

Source : MNHN, Paris

Source : MNHN, Paris

Geographical Distribution of Diplopods in Great Britain and Ireland; Possible Causal Factors

Anthony D. BARBER * & *Richard E.* JONES **

* Plymouth College of Further Education
Kings Road, Devonport, Plymouth PL1 5QG, U.K.
** 14 Post Office Road, Dersingham
Kings Lynn, Norfolk, PE31 6HP, U.K.

ABSTRACT

The locations and aspects of the habitats of Diplopoda have been recorded under the auspices of the BRITISH MYRIAPOD SURVEY Scheme since 1970 and records have been obtained from 1790 10 km squares of the British National Grid (Great Britain and islands) and 419 squares of the Irish National Grid (Ireland), a total now in excess of 30,000 species/location records. A provisional atlas was published in 1988 and a number of new records have increased our knowledge of the distribution of millipedes in these islands. The present report examines the pattern of distribution of species and the possible influence of climatic and other factors on the origins and distribution of the diplopod fauna. It is considered that a high proportion of the British and Irish fauna is likely to have arrived following the loss of the land connections with mainland Europe at the end of the last glaciation. Nevertheless there are considerable similarities with the fauna of nearby countries.

RÉSUMÉ

Répartition géographique des Diplopodes en Grande-Bretagne et en Irlande : les causes possibles.

Les localités et la nature des habitats des diplopodes des Îles Britanniques ont été répertoriées sous les auspices du BRITISH MYRIAPOD SURVEY, établissant un bilan depuis 1970 à partir de 1790 carrés de 10 km de côté, correspondant au carroyage national britannique UTM (Grande Bretagne et îles) et de 419 carrés correspondant au carroyage national irlandais UTM (Irlande). Le total des stations espèces/localités dépasse maintenant les 30 000. Un premier document a été publié en 1988 sous forme d'un atlas provisoire mais, depuis, un grand nombre de nouvelles données sont venues accroître notre connaissance sur l'inventaire et la répartition des espèces de diplopodes répertoriées dans les Îles Britanniques. Le présent travail aborde les modes de répartition des espèces, les influences possibles du climat ainsi que d'autres facteurs sur l'origine et la distribution biogéographique de la faune des diplopodes. On considère qu'une grande proportion de la faune britannique et irlandaise semble s'être constituée à la suite de la perte de continuité des terres émergées avec l'Europe continentale à la fin de la dernière glaciation. Il existe cependant de profondes similarités avec la faune des pays voisins du nord de l'Europe.

BARBER, A. D. & JONES, R. E., 1996. — Geographical distribution of diplopods in Great Britain and Ireland; possible causal factors. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 243-256. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

INTRODUCTION

A distribution recording scheme for Diplopoda alongside one for Chilopoda was launched in 1970 by the BRITISH MYRIAPOD GROUP using an itemised record card which has been described elsewhere (BARBER & FAIRHURST, 1972). A new style card was introduced in 1985. The present review concentrates on the distributional data that has been derived from this.

The record card was designed for both professional and amateur usage and a very high proportion of records were in fact obtained by non-professional but highly competent recorders working in various parts of the British Isles. Identification was checked by a panel of referees as necessary so that the level of misidentification of specimens is likely to be insignificantly low.

By the nature of the scheme, the coverage was patchy.

1. At least initially, recorders tended to collect the larger and more conspicuous species. Smaller species and soil dwelling types will be under-recorded.

2. Some areas were recorded in great detail over many years (e.g. Yorkshire) whilst others had only one or a few casual collections made there.

3. Millipedes are highly sensitive to microclimatic changes and often seasonal in their occurrence so that a species may not be found on a particular occasion even though it is common in the area.

4. Different collecting procedures may yield quite different results. For instance, pitfall trapping generally collects the larger active iuliforms, polydesmids and *Chordeuma* spp.; finding *Stygioglomeris crinita* generally requires careful hand sieving of soil.

5. Immature specimens of some species e.g. *Polydesmus* spp. and *Chordeuma* spp. cannot be determined with accuracy. These may be the only specimens of a species found in a site.

There is a substantial element of chance in records being made. For instance BLOWER (1985) wrote, "There remains no evidence that *N. minutus* (= *venustus* in the sense of Schubart, 1934) has ever occurred in Britain, but there is a possibility that it may occur". It has subsequently (as *N. kochii*) been recorded on a number of occasions and is mapped from twelve 10 km grid squares.

RESULTS OF THE SURVEY

More than 400 individual recorders participated in the scheme and collections made for other purposes were also examined and a total of more than 30,000 species/site/data records are now held. This has allowed the plotting of distribution maps based on the British and Irish national grids using the 10 km square as the unit of recording. A preliminary atlas using the then available data was published in 1988 (BRITISH MYRIAPOD GROUP, 1988).

The present discussion is based on updated versions of these maps. Many more records were made in certain areas compared with others, often with much greater detail. Such well recorded areas include Kent, Surrey, Isle of Wight, Bedfordshire, parts of S. Wales, Yorkshire, Lothians, parts of Devon, Norfolk, Suffolk. Figure 1 shows the 10 km squares from which one or more records exist.

A summary of the regional distribution of species, including occurrence on outlying islands is shown in Table 1 and examples of distribution patterns are shown in Figures 7-18. An updated atlas of distribution will be published in due course, meanwhile records are held on cards and on the database at the Environmental Information Centre, Monks Wood, Huntingdon.

Nomenclature is as in BLOWER (1985) except that a new species, *Anthogona britannica*, is since described by GREGORY *et al.* (1994).

Source : MNHN, Paris

TABLE 1. — Distribution in various areas of the British Isles (X = presence in 1 or more 10 km grid square). Based on data from the MILLIPEDE SURVEY SCHEME. She = Shetland Islands, Ork = Orkney Islands, WIs = Western Isles, C&S = Caithness & Sutherland (North Scotland), Sco = Scotland, Ire = Ireland, IOM = Isle of Man, L&Y = Lancashire & Yorkshire, Sou = Southern England (South of line from Mersey - Wash, including SE and SW), Wal = Wales, SWE = South West England (Devon & Cornwall), KSS = Kent, Surrey, Sussex (extreme SE), CIs = Channel Islands (Jersey, Guernsey,etc,). NB: Shetland, Orkney, Western Isles, Caithness & Sutherland, Isle of Man and Channel Islands have relatively few records.

Species	She	Ork	WIs	C&S	Sco	Ire	IOM	L&Y	Sou	Wal	SWE	KSS	CIs
P. lagurus					X	X	X	X	X	X	X	X	X
G. marginata					X	X	X		X	X	X	X	
S. crinita					X	X		X	X	X		X	
A. gibbosa						X							
T. lobata									X				
P. germanicum									X			X	
C. rawlinsii					X	X		X	X	X	X	X	
N. polydesmoides		X	X	X	X	X	X	X	X	X	X		
B. melanops						X			X	X	X	X	
B. bagnalli/bradae						X		X	X				
C. silvestre									X		X		
C. proximum						X			X	X	X	X	X
M. gallica					X	X			X	X	X		
M. scutellare					X	X		X	X	X	X		
T. littoralis									X	X	X	X	
N. varicorne				X	X	X		X	X	X	X	X	
P. fuscus	X	X		X	X	X		X	X	X	X	X	X
C. palmatus					X	X		X	X	X	X	X	
N. kochii								X	X	X			
B. guttulatus					X	X	X	X	X	X	X	X	X
A. pallidus	X	X			X	X		X	X	X		X	
B. tenuis	X	X			X	X		X	X	X	X	X	
O. sabulosus				X	X	X	X	X	X	X	X	X	X
T. niger				X	X	X	X	X	X	X	X	X	X
A. nitidus					X	X		X	X		X	X	
C. londinensis					X	X			X	X		X	
C. caeruleocinctus					X	X		X	X	X	X	X	
C. vulnerarius						X		X	X	X	X	X	
C. latestriatus	X	X	X	X	X	X	X	X	X	X	X	X	
C. britannicus				X	X	X	X	X	X	X	X	X	
C. punctatus	X	X	X	X	X	X	X	X	X	X	X	X	
C. parisiorum						X		X	X	X	X	X	
C. truncorum									X			X	
E. armatus									X		X		
J. scandinavius				X	X	X	X	X	X	X	X	X	
O. pilosus				X	X	X	X	X	X	X	X	X	X
L. belgicus									X	X	X	X	X
L. kervillei									X		X	X	
M. pratensis									X			X	
B. pusillus				X	X	X	X	X	X	X	X	X	X
U. foetidus									X				
A. britannicus									X		X		
P. angustus		X	X	X	X	X	X	X	X	X	X	X	X
P. testaceus									X		X	X	
P. inconstans	X	X	X	X	X	X	X	X	X	X	X	X	
P. gallicus					X	X		X	X	X	X	X	
P. denticulatus	X			X	X	X		X	X	X	X	X	
B. superus		X	X	X	X	X	X	X	X	X	X	X	X
M. palicola					X	X		X	X	X	X	X	
O. albonanus					X	X		X	X	X	X	X	
S. italica						X			X	X		X	

Source : MNHN, Paris

DISTRIBUTION PATTERNS IN BRITAIN

Geographical

A crude analysis for the commonest species is displayed in Table 2. For the purpose of this, Great Britain is divided into a series of regions based on the 100 km grid squares (Fig. 2). For each species the total 10 km squares for that species is taken as a percentage of the total 10 km squares in that region for which records exist. This will underestimate smaller and more difficult to find forms and will also reflect the relative intensity of collecting. Thus, for instance, the northern part of Britain will have disproportionately more larger species recorded because much collecting there so far has been of a casual and superficial nature. For this reason, the values should be treated with great caution. Nevertheless they do show up the pronounced relative scarcity of *Ommatoiulus sabulosus* and *Julus scandinavius* in the southeast and an almost opposite pattern for *Cylindroiulus caeruleocinctus* which is relatively rarely found in the southwest. The north-south pattern of some species is also shown.

TABLE 2. — Analysis of records for the commonest species for regions of the British Isles as a percentage of total 10 km recorded squares for the region. NSco = Northern Scotland, SSNE = Southern Scotland & Northern England, MidE = Midland England, East = Eastern England, SEE = South East England, SWE = South West England, Wal = Wales, GBT = Total Great Britain, Ire = Ireland.

Species	NSco	SSNE	Y/L	MidE	East	SEE	SWE	Wal	GBT	Ire
P. lagurus									9.6	0.7
G. marginata	0.0	36.8	53.5	56.0	46.8	67.3	59.7	54.1	46.3	23.9
N. polydesmoides	9.2	27.4	55.1	46.0	51.7	55.6	38.1	45.2	40.1	32.5
C. proximum	0.0	0.5	0.0	1.3	0.5	9.3	8.3	42.6	6.0	0.2
N. varicorne	3.9	7.3	25.7	24.6	18.9	30.9	27.6	15.5	18.9	1.7
P. fuscus	27.5	36.8	58.3	41.9	57.9	47.8	54.6	55.8	47.6	18.1
B. guttulatus	2.4	9.4	21.9	38.2	24.4	34.6	25.4	27.7	23.0	11.3
O. sabulosus	32.7	29.9	34.8	23.9	32.3	5.9	28.2	30.4	26.9	4.8
T. niger	22.7	91.4	90.4	75.7	80.1	67.3	55.8	68.9	66.1	28.9
C. caeruleocinctus	4.8	5.3	4.9	18.4	17.9	33.7	5.0	2.7	11.1	0.2
C. punctatus	57.0	63.9	85.6	83.5	73.6	79.5	76.2	63.5	73.1	45.1
C. britannicus	5.3	13.5	17.6	22.3	7.0	19.0	9.4	20.2	14.6	10.0
J. scandinavius	23.7	28.8	49.7	32.0	34.8	6.8	54.1	47.3	33.4	6.9
O. pilosus	24.6	25.7	50.3	47.9	37.8	39.5	35.9	60.8	39.3	31.0
P. angustus	31.4	38.2	75.9	61.5	64.7	59.0	47.0	58.1	53.8	27.0
P. inconstans	6.8	8.7	12.3	10.7	11.4	15.6	3.3	2.7	9.3	6.7
P. gallicus	0.0	1.4	5.3	27.5	18.9	32.7	13.8	21.6	15.1	24.1
P. denticulatus	2.9	3.1	11.2	11.3	23.9	16.6	13.3	29.1	12.7	2.2
B. superus	8.2	16.3	32.1	31.1	43.3	54.0	42.0	27.0	30.9	10.0
M. palicola									8.4	0.7
O. albonanus									7.1	0.7

Species with a southeasterly distribution include *C. caeruleocinctus* (above) which may be increasing its range and *Stosatea italica* which is beginning to be found in a variety of areas in England, Wales and Ireland having been found fairly widely in East Kent originally, again presumably spreading, markedly synanthropic in many cases and found sporadically in rather superficial habitats. Also *Polydesmus testaceus* known only from Kent with one older Cornish record, *Metaiulus pratensis*, originally found in Kent and Sussex and recently found again in Kent, presumably mostly soil dwelling, *Polyzonium germanicum* mostly from Kent and *Cylindroiulus londinensis* often found around the London area, commonly in synanthropic sites but also recorded elsewhere in England.

Correspondingly, in the southwest *Enantiulus armatus*, so far found only in one area in Devon, *Chordeuma silvestre* from Cornwall, *Chordeuma proximum*, widespread in southwest

Source : MNHN, Paris

England, in much of the rest of southern England and very common in South Wales. The two *Leptoiulus* spp., *L. belgicus* and *L. kervillei* are typically southwestern but records across southern Britain are known and *L. belgicus* has been found in Ireland. Several species have not been found commonly in the southwest, if at all. These include *Archiboreoiulus pallidus*, *Craspedosoma rawlinsii*, *Cylindroiulus caeruleocinctus* and *C. londinensis*. *Brachychaeteuma melanops* is a distinctly southern species whilst the other two British *Brachychaeteuma* species seem to have a more central/northern tendency in general.

There is a distinct group of species apparently rare or possibly absent in northern Scotland. These include *Glomeris marginata*, *Brachychaeteuma* spp., *Chordeuma* spp., *Cylindroiulus caeruleocinctus, C. londinensis*, possibly *C. parisiorum, Blaniulus guttulatus, Choneiulus palmatus* and *Polyxenus lagurus*, although, especially given its distribution elsewhere in Europe, the latter may simply have been overlooked, something that may also be true of some other species listed. A number of species appear possibly to be absent from the Shetland Islands, etc. (Table 1).

Other factors

Apart from the fact that we do not really know the exact regional distribution of species, there are certain other factors which seem to affect where they are found. A frequently quoted influence is the presence of calcareous soils; in fact the number of species in Britain which show a clear calcicole tendency is quite small. *Stygioglomeris crinita* does appear to favour such soil; it may in fact be very widespread but the difficulty in finding it makes it impossible at the present time to be certain. *Stosatea italica* and possibly *Polydesmus testaceus* are also possible calcicoles. The other likely species restricted in this way is *Macrosternodesmus palicola*. *Cylindroiulus caeruleocinctus*, often found on calcareous soils, does not appear to be confined to them.

There are also a considerable number of species which favour agricultural and/or synanthropic sites. In the first category are possibly *Archiboreoiulus pallidus*, *Brachydesmus superus*, and maybe *Metaiulus pratensis*. Of the synanthropes many are also found elsewhere but they include *B. guttulatus*, *Brachychaeteuma* spp., *B. superus* (?), *Choneiulus palmatus* (?), *Cylindroiulus britannicus* (?), *C. londinensis*, *C. vulnerarius*, *C. truncorum*, *Nopoiulus kochii* (?), *Ophiodesmus albonanus*, *Polydesmus angustus* (?). *Thalassisobates littoralis* is a purely littoral species whilst *Cylindroiulus latestriatus* is a common coastal species but also found inland.

The very common *Cylindroiulus punctatus* is a distinct woodland species and is generally only found in woods, close to them or on the site of former woodland. Possibly other species show this tendency in a less pronounced form.

There are some species for which so few records exist that it is difficult to see a clear pattern. These include *Unciger foetidus* (one Norfolk site), *Anthogona britannica* (one Devon site, GREGORY *et. al.* , 1994, *Trachysphaera lobata* (Isle of Wight) and *Adenomeris gibbosa* (Dublin). Correspondingly there are species which seem to occur in a wide variety of habitats over a wide area. *Oxidus gracilis* and several other species are only known from glasshouses.

COMPARISON WITH OTHER AREAS IN EUROPE

Much of the British diplopod fauna is common with that of nearby areas of Western Europe. For some species, the British Isles seem to be the centre or one of the centres of their occurrence, a topic which is discussed by DOOGUE *et al.* (1993) with special reference to Ireland. Table 3 shows British species and their occurrence elsewhere on the continental mainland.

Source : MNHN, Paris

TABLE 3. — Distribution of species in various areas of Europe based on available information (X = presence out of doors). Based on DOOGUE *et al.* (1993), EASON (1970), ENGHOFF (1974 & pers. comm.), JEEKEL (1978), KIME (1990, 1992 and pers. comm.), LINDROTH (1957), MEIDELL (1972, 1979), MEIDELL & SOLHY (1979), PALMEN (1949), REMY & HOFFMANN (1959), etc. **U. foetidus* and *A. britannica* are known from single localities only in E and SW England respectively. Ice = Iceland, Fae = Faeroes, ShO = Shetland & Orkney, GBT = Great Britain, Ire = Ireland, Nor = Norway, Den = Denmark, NNW = North West Netherlands, NSW = South Netherlands, BeL = Belgium & Luxembourg, NFr = North France, Ame = Americas; var = various.

Species	Ice	Fae	ShO	GBT	Ire	Nor	Den	NNW	NSW	BeL	NFr	Ame
P. lagurus				X	X	X	X	X		X		
G. marginata				X	X	X	X	X	X	X	X	
S. crinita				X						X		
A. gibbosa					X							
T. lobata				X								
P. germanicum				X			X				X	
C. rawlinsii				X	X	X	X			X	X	
N. polydesmoides		X	X	X	X	X		X	X	X	X	
B. melanops				X	X							
B. bagnalli/bradae				X	X		X	X				
C. silvestre				X					X	X	X	
C. proximum				X	X						X	
M. gallica				X	X	X			X	X	X	
M. scutellare				X	X							
T. littoralis				X								
N. varicorne				X	X	X	X	X	X	X		
P. fuscus	X	?	X	X	X	X	X	X	X	X	X	X
C. palmatus				X	X	X	X	X	X	X		X
N. kochii				X		X	X	X	X	X		X
B. guttulatus	?			X	X	X	X	X	X	X		X
A. pallidus		X	X	X	X	X			X			
B. tenuis			X	X	X	X	X	X	X	X		
O. sabulosus				X	X	X	X	X	X	X	X	
T. niger				X	X			X	X	X	X	
A. nitidus				X			X	X	X	X	X	
C. londinensis				X	X	X					X	
C. caeruleocinctus				X	X		X	X	X	X		X
C. vulnerarius				X	X			X	X	X		
C. latestriatus		X	X	X	X	X	X	X	X	X		
C. britannicus				X	X	X	X	X				X
C. punctatus			X	X	X	X	X	X	X	X	X	X
C. parisiorum				X	X		X	X		X	X	
C. truncorum				X			X	X	X	X	X	X
E. armatus				X								
J. scandinavius				X	X	X	X	X	X	X	X	
O. pilosus				X	X	X	X	X				
L. belgicus				X	X				X	X	X	
L. kervillei				X					X	X	X	
M. pratensis				X								
B. pusillus				X	X		X	X	X	X		X
U. foetidus				*		X	X	X				
A. britannica				*								
P. angustus			X	X	X	X	X	X	X	X	X	
P. testaceus				X					X	X	X	
P. inconstans	X		X	X	X	X	X	X	X	X	X	X
P. gallicus				X	X					X		
P. denticulatus				X	X	X	X	X	X	X		X
B. superus	X	X	X	X	X	X	X	X	X	X	X	X
M. palicola				X	X		X	X	X	X		
O. albonanus				X	X		X	X	X	X		X
S. italica				X	X			X	X			
Other species						3	9	5	4	16	var	

Source : MNHN, Paris

Almost all species recorded from Norway occur in Britain with the exception of *Polydesmus complanatus* (Britain has *P. angustus*) and *Leptoiulus proximus* but a number of British species have not yet been found there. Eastern Fennoscandia similarly has a high proportion of "British" species (PALMEN, 1949) but with other more eastern ones. Denmark, with 37 outdoor species, includes 9 not found as yet in Britain. The Netherlands has a somewhat similar fauna to eastern Britain, several not found in Britain, with southeast Netherlands having several species only found in southern Britain. Data for Belgium, Luxembourg and northern France shows most British forms although species such as *Adenomeris gibbosa*, *Trachysphaera lobata*, *Enantiulus armatus* and *Metaiulus pratensis* seem to come from further south. There are about 16 species from the Belgium, Luxembourg area which do not occur in Britain as far as is known as present.

KIME (1990) has mapped a number of species in Europe and has demonstrated some curious aspects of this such as the disjunct distribution of *Ophyiulus pilosus* with a seeming gap in its occurrence between Britain and Scandinavia/North Germany/Poland and Bavaria/Italy. He demonstrates *Nanogona polydesmoides* as Britain/France, *Chordeuma proximum* similarly but *C. silvestre* (only here known from Cornwall) with a much wider occurrence. It would be helpful to have more data from northern France for comparative purposes.

POSSIBLE CAUSAL FACTORS IN DISTRIBUTION

Present Day Climate

The climate of the British Isles is usually described as Atlantic or Oceanic with comparatively low temperatures in summer and comparatively high in winter compared with nearby continental Europe. But within this description is considerable local variation, including the influence of the sea in coastal areas, altitude in so called "Highland Britain" (mostly western and northern areas) and the "heat island" effect of urban areas which may permit the survival of species outside their normal range.

Mean annual rainfall varies from below 500 mm in part of Eastern England to more than 1600 mm in areas of the west and up to more than 2400 mm in some mountainous areas, with a general tendency for much of mid-southern, southwestern and northwestern England together with Wales and Scotland to have 800 mm or more, as does Ireland (Fig. 3). Given the sensitivity of myriapods to moisture one might seek some correlation with this but there is no obvious one for most species except perhaps, in England and Wales, *Chordeuma proximum*.

Temperature is frequently a factor influencing animal distribution, affecting as it may do survival for individuals, availability of food and breeding cycles. High summer (July) isotherms tend to run in an approximately east-west direction (Fig. 5) and there are a number of species referred to which appear either to have a southerly distribution or are, as in the case for instance of *Glomeris marginata*, absent from apparently suitable habitats in northern areas of Scotland. Until more data is available on the effect of temperature on breeding cycles etc. in diplopods one can only speculate on the causal factors here.

DAVID (see this volume) describes how *G. marginata* in an oak forest in southern France tends to move into the soil in winter, confirming previous work that suggests that it is in fact cold intolerant. SUSTR (see this volume) describes how *G. marginata* has a much lower metabolic rate than *G. balcanica* and *G. hexasticha* at low temperatures, which may mean that in cold conditions it is unable to assimilate effectively and would therefore be unable to tolerate these conditions for any length of time.

January mean isotherms (Fig. 4) tend to run in a more north-south direction with the western areas relatively warmed by the influence of the sea whilst the eastern parts have a more

Source : MNHN, Paris

"continental" colder drier climate. There do not appear to be clear correlations with species here but the more extreme, drier climate of the south-east, especially Kent, may favour, either directly or by excluding competitors, certain species such as *Polyzonium germanicum*, *Stosatea italica*, *Polydesmus testaceus*, and *Metaiulus pratensis*.

Past Climates and Land Bridges

Conditions during the Devensian (Würm) glaciation were such that much of the British Isles were covered with ice sheets, reaching at their maximum the whole of the area north of South Wales and North Yorkshire and the Norfolk coast. At the same time mainland Britain was joined both to Ireland and to mainland Europe by land bridges. The area south of the ice sheets was subject to periglacial conditions. Under such circumstances, the diplopod fauna was likely to have been extremely sparse if not entirely absent in the present day area of the British Isles. Sub-arctic conditions would have prevailed down to about 10,000 BP following the climatic improvement of the Aller interstadial. A temperature with a July mean below +10 is quoted for this Younger Dryas phase (NILSSON, 1982). This period was then followed by the transition to Pre-Boreal and the re-establishment of forests. VAN DER HAMEN *et al.* (1971) describe conditions as having reached mixed deciduous oak forest in the Netherlands by 8,000 BP.

Such conditions would clearly favour the spread of species north from climatic refuges. However, rising sea levels led to the breaking through at the Dover Straits about 9,600 BP and between East Anglia and the Netherlands in 8,600 BP (JONES, 1985). After this period the only dispersal across the English Channel/North Sea would be by passive transport or human activity. There is thus a period of about 400-1400 years during which species could re-invade Britain directly. However, the effective separation of Ireland must be placed earlier and this has been considered to account for the absence in that country of some species of animals (e.g. certain amphibians and reptiles) present on mainland Britain.

A number of species of diplopod do occur in fairly northern locations in Europe. PALMEN (1949) reported *Proteroiulus fuscus* north of latitude 66 degrees with *Cylindroiulus latestriatus* and *Ommatoiulus sabulosus* north of 64 degrees and *Polyxenus lagurus*, *Polydesmus denticulatus* and *Polyzonium germanicum* all north of 62 degrees in Eastern Fennoscandia. MEIDELL (1972) included *P. lagurus*, *P. fuscus*, *Polydesmus complanatus* (which does not occur in Britain), *C. latestriatus* and two species usually regarded as synanthropes in northern Europe, *Blaniulus guttulatus* and *Cylindroiulus londinensis* as his most northerly recorded species. EASON (1970) reports three species, *Brachydesmus superus*, *Polydesmus coriaceus* and *P. fuscus* with possibly *B. guttulatus* from Iceland. These latter must have all presumably arrived in some way from other parts of Europe but their existence in Iceland indicates a degree of tolerance of local conditions there.

GOLOVATCH (1992) in his survey of the Russian Plain describes *P. fuscus* from tundra, *P. fuscus, P. germanicum* and two other species from northern taiga; these plus *P. lagurus, O. sabulosus* and five other species from mid taiga, and amongst species from southern taiga, *P. denticulatus* and *N. varicorne*.

FIG. 1. — 10 km grid square distribution: total records for the British Isles.

FIG. 2 . — Regions used for Table 2 analysis.

FIG. 3. — British Isles: Mean Annual Rainfall in mm (based on ATKINSON & SMITHSON *in* CHANDLER & GREGORY, 1976).

FIG. 4. — British Isles: Mean January Temperatures 1941 - 70 (reduced to sea level) (after TOUT *in* CHANDLER & GREGORY, 1976).

FIG. 5. — British Isles: Mean July Temperatures 1941 - 70 (reduced to sea level) (after TOUT *in* CHANDLER & GREGORY, 1976).

FIG. 6. — British Isles: Fig of the Main Devensian ice advance (solid line) (after SPARKS & WEST, *in* EVANS, 1975).

Source : MNHN, Paris

Source : MNHN, Paris

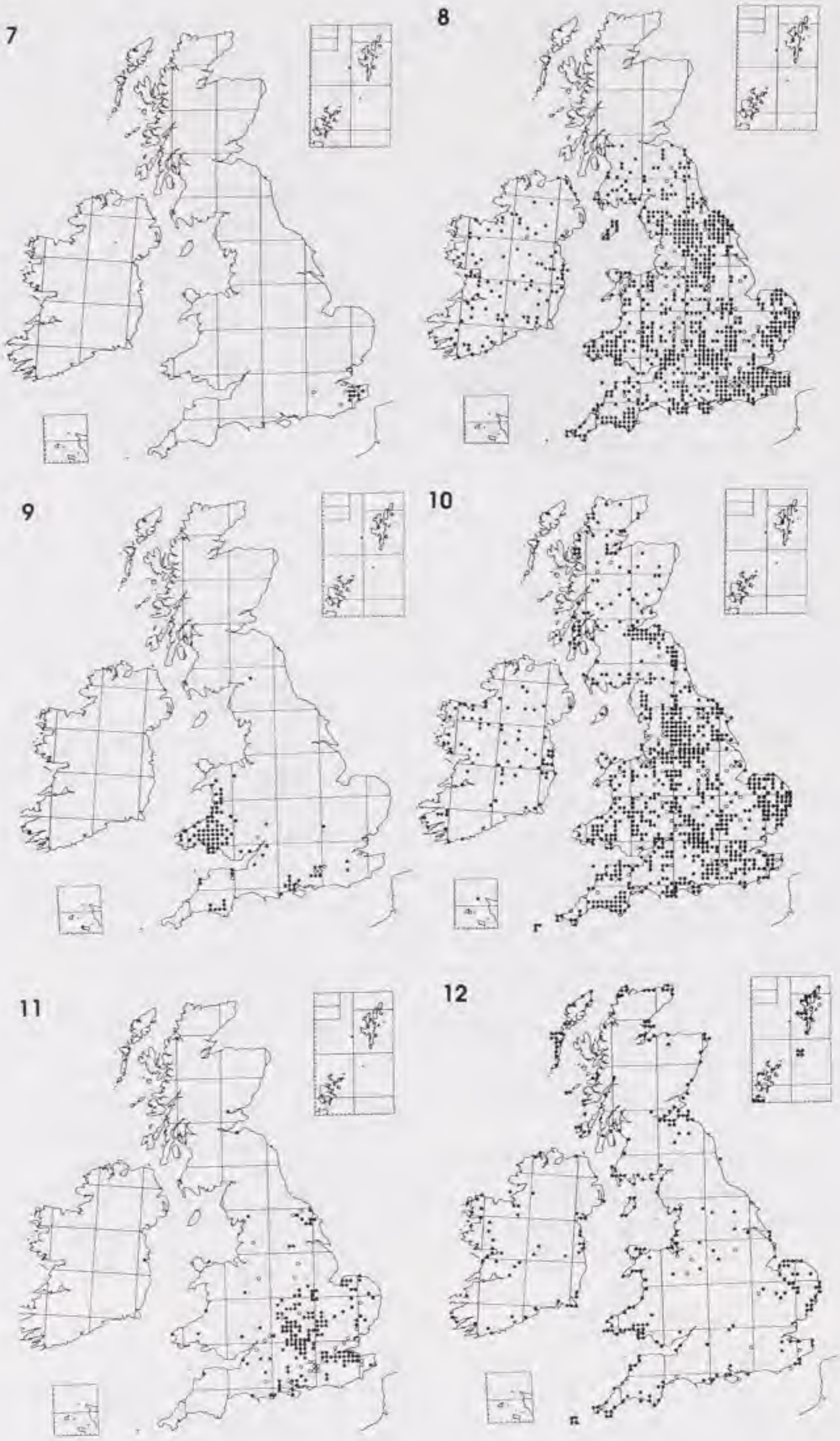


FIG. 7-18. — 10 km distribution Figs of selected species: 7. *Polyzonium germanicum*, 8. *Glomeris marginata*, 9. *Chordeuma proximum*, 10. *Proteroiulus fuscus*, 11. *Cylindroiulus caeruleocinctus*, 12. *C. latestriatus*, 13. *C. londinensis*, 14. *C. punctatus*, 15. *Julus scandinavius*, 16. *Ophyiulus pilosus*, 17. *Leptoiulus kervillei*, 18. *Enantiulus armatus*.

Source : MNHN, Paris

13

14

15

16

17

18

Source : MNHN, Paris

Clearly there is therefore a possibility of some of the above species being able to tolerate conditions in southern Britain during glacial times or at least to cross the land bridge before it broke down. Most of these species are widespread in both Britain and Ireland (although, for some reason, *P. germanicum* is confined to the extreme southeast).

Once the land bridges had broken, then entry to the British Isles was possible only by either passive transport by rafting or by being brought in accidentally by human activity. Rafting is not easy to demonstrate although PALMEN (1949) refers to *P. fuscus* on driftwood in S. Finland and suggest that such passive transport combined with parthenogenesis could account for its occurrence on outlying islands.

Evidence for possible entry of animals via land bridges or survival during periglacial conditions is provided by reptiles and amphibians, especially the latter which would be highly vulnerable to salt water. These animals are of sufficient size that the likelihood of accidental transport by human activity will be far less than that for soil invertebrates such as diplopods. Six reptiles and the same number of amphibians are recorded from the British isles together with two recent successful introductions, *Rana esculenta* and *R. ridibunda*. These latter, together with the fact that other species have occurred in the past (HOLMAN, 1993), suggest that it is historical factors that have determined the relative paucity of British species. Of the British forms, only 1 reptile and 3 amphibians occur in Ireland. One of these, *Bufo calamita* seems somewhat anomalous and has been a field for some speculation (see, e.g. BEBEE, 1984). The lower number of species fits in with the idea of an earlier isolation of Ireland. Of the species that do occur these all occur in Scandinavia (ARNOLD & BURTON, 1978) with *Lacerta vivipara* and *Rana temporaria* extending to the extreme north and *Triturus vulgaris* to mid Norway/Sweden. *Bufo sp*., *R. temporaria*, *L. vivipara* and the widespread British snake *Natrix natrix* are known from Devensian deposits.

Given that the present herpetological fauna was in place by about 8,800 BP (HOLMAN, 1993), by which time separation would have been occurring, we could visualise that a relatively small number of diplopod species, derived from adjacent areas of Europe, was already present. These might have included *Polyxenus lagurus*, *Proteroiulus fuscus*, *Nemasoma varicorne*, *Ommatoiulus sabulosus*, *Cylindroiulus latestriatus*, *Polydesmus denticulatus* and others.

Other species would arrive either by rafting on tree trunks or other material or be brought in accidentally with plant material or soil by human activity (see below).

Whatever the mode of their arrival, the improvement in climate towards the so-called Climatic Optimum of about 7,000 - 5,000 BP, when mean temperatures were about 2-3 degrees higher than at present, would have covered much of the country. Subsequent climatic changes such as the climatic oscillation around 5,500 - 5,000 BP and the so called "Little Ice Age" AD1550 - 1850 may well have brought about later contractions in range. The patchy distribution one now sees for instance of species widespread in France such as *Enantiulus armatus* and the *Leptoiulus* spp. could be vestiges of a once wider occurrence.

Entry by Rafting and Human Influence

It is difficult to give convincing evidence for rafting by organisms such as millipedes but it has certainly been suggested for a variety of animal types for oceanic crossing (see for instance, GARDNER, 1985 referring to geckos in the Seychelles and Mascarenes). Littoral or coastal species (such as *Cylindroiulus latestriatus*, a very widespread island species) are most easily transported in this way and parthenogenesis as in the case of *Proteroiulus fuscus* would assist. However, a variety of species from woodland might be transported as a result of exceptional conditions e.g. storm damage in coastal areas.

Human influence has undoubtedly assisted in the spread of some species of recent arrival such as *Cylindroiulus vulnerarius* and human introduction of invertebrates to islands is widely quoted (see e.g. JONES & PRATLEY, 1987). Human activity undoubtedly plays a part in the

Source : MNHN, Paris

spread of soil animals. A recent example is the New Zealand planarian, *Artioposthia triangulata* in Britain (J. FREW, pers. comm.) first recorded in Scotland in 1965 but with 416 records by 1992.

The occurrence of myriapods in isolated islands such as Iceland as well as the islands around Britain or those of Denmark (ENGHOFF, 1974) are best explained in terms of transport either by rafting or human influence. The very high proportion of British species in Ireland, where land connection would have been lost soon after the disappearance of the ice, cannot be convincingly explained by reference solely to land bridges but must involve transport across water.

LINDROTH (1957) has listed 17 species of diplopod known from Europe which occur in the Americas, 16 of which (including *Oxidus gracilis*, a greenhouse form of tropical origin) are found in Britain. Of the 18 species of millipede reported from Newfoundland 16 are regarded as introduced forms from Europe with 37 of the 42 isopods and myriapods falling into this category. Clearly such species have been introduced by human influence and presumably could have reached the British Isles in the same way. LINDROTH gives five criteria for an introduced species; it is difficult to apply these to the present situation except for very clearly recent arrivals or species with clearly synanthropic habits such as *Cylindroiulus vulnerarius* or *C. truncorum*. If glacial and periglacial conditions and subsequent breakdown of land bridges had left a number of vacant niches then presumably these could be filled by incoming species with the appropriate characteristics. It is difficult to conceive of common species of woodland and other habitats such as *Glomeris marginata* and *Tachypodoiulus niger* as other than "native" species. In this case then opportunities for crossing the land bridge in the wake of the ice must have been rather greater than we have suggested.

Cylindroiulus londinensis, common in much of France, is an example of what may be an "old" introduction which has or is still spreading out from the London area, largely in synanthropic or semi-synanthropic areas.

CONCLUSIONS

We would suggest that a fairly high proportion of British diplopods are likely to be forms which may have arrived in the period after the breakdown of the land bridges between Britain and Ireland and between mainland Europe and Britain. Although climatic and other conditions are not identical with nearby areas the fauna is similar apart from some more eastern and southern species, and the occurrence of species both on islands and in America confirms their ability to cross water. There are likely to have been subsequent changes in distribution due to climatic changes, the introduction of new species, habitat destruction and possibly to other as yet imperfectly understood factors, such as those quoted by FORD (1982) for butterflies.

ACKNOWLEDGEMENTS

Clearly this scheme would not have been possible without all those too numerous to mention individually contributed records, to past scheme organisers C. P. FAIRHURST (responsible for the origin of the two myriapod recording schemes) and D. T. RICHARDSON (who also organised the highly detailed recording of the largest area, Yorkshire), to D. DOOGUE in Ireland, J. G. BLOWER, author of the standard key and of many identifications, A. N. KEAY for much help and advice, R. D. KIME of Brussels, H. ENGHOFF of Copenhagen and to P. T. HARDING of the British Biological Records Centre. We would also acknowledge C. M. MOISER for comments and references on reptiles and amphibians.

REFERENCES

ARNOLD, E. N. & BURTON, J. A., 1978. — *A Field Guide to the Reptiles and Amphibians of Britain and Europe*. London, Collins. 242 pp.

BARBER, A. D. & FAIRHURST, C. P., 1974. — A habitat and distribution recording scheme for Myriapoda and other invertebrates. *Symp. Zool. Soc. Lond.*, **32** : 611-619.

Source : MNHN, Paris

BEBEE, T. J. C., 1984. — Possible Origins of Irish natterjack toads (*Bufo calamita*). *Brit. J. Herpetology*, **6** : 398-401.

BLOWER, J. G., 1985. — *Millipedes* (Synopses of the Br. Fauna NS, **35**). London, E. J. Brill & W. Backhuys, 242 pp.

BRITISH MYRIAPOD GROUP, 1988. — *Preliminary Atlas of the Millipedes of the British Isles*. Huntingdon, NERC. 65 pp.

CHANDLER, T. J. & GREGORY, S., 1976. — *The Climate of the British Isles*. London/New York, Longmans. 390 pp.

DOOGUE, D., FAIRHURST, C. P., HARDING, P. T.& JONES, R. E., 1993. — A Review of Irish Millipedes (Diplopoda). *In* : M. S. COSTELLO, *Biogeography of Ireland: past, present and future. Occ. Publ. Ir. biogeog. Soc.* **2**.

EASON, E. H., 1970. — The Chilopoda and Diplopoda of Iceland. *Ent. scand.*, **1** : 47-54.

ENGHOFF, H., 1974. — Om tusindbenenes udbredelse i Danmark (Diplododa). *Ent. Meddr.*, **42** : 21-32.

EVANS, J. G., 1975. — *The Environment of Early Man in the British Isles*. London, Unwin. 216 pp.

FORD, J. J., 1982. — *The Changing Climate: Responses of the Natural Flora and Fauna*. London, Allen & Unwin. 190 pp.

GARDNER, A. S., 1985. — Viability of the eggs of the day-gecko *Phelsuma sundbergi* in sea water. *Brit. J. Herpetology*, **6** : 435-436.

GOLOVATCH, S. I., 1992. — Some patterns in the Distribution and Origin of the Millipede Fauna of the Russian Plain (Diplopoda). *Ber. nat.-med. Verein Innsbruck*, **510** : 373-378.

GREGORY, S. J., JONES, R. E. & MAURIÈS, J. P., 1994. — A new species of Millipede (Myriapoda, Diplopoda, Chordeumatida) from the British Isles. *J. nat. Hist.*, **28**, 1993 : 47-52.

HOLMAN, J. A., 1993. — British Quaternary herpetofaunas: a history of adaptations to Pleistocene disruptions. *Herpetological J.*, **3** : 1-7.

JEEKEL, C. A. W., 1978. — Voorlopige atlas van de verspreiding der Nederlandse Miljoenpoten (Diplopoda). *Verslagen technische Gegevens Inst. taxon. zool. Univ. Amsterdam*, **15** : 1-69.

JONES, D. K. C., 1985. — Shaping the Land: The Geomorphological Background. *In* : S. R. J. WOODELL, *The English Landscape, Past, Present, and Future*. Oxford, Oxford University Press.

JONES, R. E. & PRATLEY, P., 1987. — Myriapods of the Isles of Scilly. *Bull. Br. Myriapod Group.*, **4** : 7-15.

KIME, R. D., 1990. — *Fauna Europaea Evertebrata: A Provisional Atlas of European Myriapods Part 1*. Luxembourg, European Invertebrate Survey. 109 pp.

KIME, R. D., 1992. — On Abundance of West European Millipedes (Diplopoda). *Ber. nat.-med, Verein Innsbruck*, **510** : 393-399.

LINDROTH, C. H., 1957. — *The Faunal Connections between Europe and North America*. New York/Stockholm, Wiley/Almqvist & Wiskell, 326 pp.

MEIDELL, B. A., 1972. — En faunistisk undorsokelse avyte Harangerfjordens myriapod fauna og en oversikt over norske myriapoders taxonomiske og dyregografiske status. Thesis, Bergen, University of Bergen (Maps given *in* The distribution of Norwegian myriapods as known to 1972 with a revised list of published papers devoted to the same subject. Zool. Museum, University of Bergen.

MEIDELL, B. A., 1979. — Norvegian Myriapods: Some Zoogeographical Remarks. *In* : M. CAMATINI, M. *Myriapod Biology*. London, Academic Press : 195-202.

MEIDELL, B. A. & SOLHY, T., 1979. — Terrestrial Invertebrates of the Faroe Islands:VI Centipedes and Millipedes (Chilopoda and Diplopoda). *In* : A. MINELLI, *Proceedings of the 7th International Congress of Myriapodology*. Leiden, Brill. : 413-427.

NILSSON, T., 1982. — *The Pleistocene*. Dordrecht/Boston/London, Reidel. 651 pp.

PALMEN, E., 1949. — The Diplopoda of Eastern Fennoscandia. *Ann. Zool. Soc. "Vanamo"*, **13** : 1-54.

REMY, P. & HOFFMANN, J., 1959. — Faune des Myriapodes du Grand-Duché de Luxembourg. *Arch. Sect. Sci. Inst Gr. Ducal Luxembourg*, **26** : 199-236.

VAN DER HAMEN, T., WIJMSTRA, T. A. & ZAGWIJN, W. H., 1971. — Floral Record of the Late Cenozoic in Europe. *In* : K. K. TUREKION, *The Late Cenozoic Glacial Ages*, Newhaven, Yale University. Press. 606 pp.

Source : MNHN, Paris

Millipedes Recorded in the Grand Duchy of Luxemburg

Richard Desmond Kime

Institut Royal des Sciences Naturelles de Belgique
Rue Vautier 29, B-1040 Brussels, Belgium

ABSTRACT

Knowledge of the occurence and distribution of millipedes in the Grand Duchy of Luxemburg is reviewed. To date 36 species have been recorded there. Regional variation is taken into account and the differences between the relatively higher Oesling, a palaeozoic massif of Devonian age, and the lower-lying Gutland of Secondary age are emphasised. Larger and longer-lived iteroparous species of millipedes are associated with open sites; the reasons for this are discussed. Comments are made on the phenology of some species.

RÉSUMÉ

Diplopodes répertoriés dans le Grand-Duché de Luxembourg.

Les peuplements de diplopodes édaphiques ont été étudiés dans plusieurs sites du Grand-Duché de Luxembourg. Une liste de 36 espèces répertoriées dans le pays est donnée. La répartition des espèces est liée aux diverses régions luxembourgeoises et surtout à la nature des roches mères. Le résultat des échantillonnages fait apparaître l'importance relative des iulides dans les sites ouverts. Les raisons en sont discutées. De nouvelles données sur la phénologie de certaines espèces sont commentées.

INTRODUCTION

A list of millipedes from the Grand Duchy of Luxemburg was published by Joseph Hoffmann (Remy & Hoffmann, 1959) and consisted of 36 species. None of the material collected at this time is to be found in the Luxemburg Natural History Museum. In 1982, occasional collecting began again and from 1988 onwards the Museum has carried out an intensive programme of pitfall trapping under the direction of Marc Meyer. Several invertebrate taxa are being studied. This paper is intended to compare recent millipede records with the list of species found by Hoffmann (see Table 1) and takes into account regional variations which remain to be analysed in more detail in the next few years. Some trends are so apparent that they may be commented upon at this stage.

Kime, R. D., 1996. — Millipedes recorded in the Grand Duchy of Luxemburg. *In*: Geoffroy, J.-J., Mauriès, J.-P. & Nguyen Duy - Jacquemin, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 257-263. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

TABLE 1. — Check-list of the 36 millipede species recorded in the Grand Duchy of Luxemburg during the 50's, compared with recent collections.

By HOFFMANN	RECENTLY
Polyxenus lagurus (Linné)	
Glomeris conspersa C. L. Koch	
Glomeris hexasticha intermedia Latzel	*Glomeris hexasticha intermedia*
Glomeris marginata (Villers)	*Glomeris marginata*
Blaniulus guttulatus (Fabricius)	
Proteroiulus fuscus (Am Stein)	
Choneiulus palmatus (Nemec)	
Nopoiulus kochii (Gervais)	
Archiboreoiulus pallidus Brade-Birks	*Archiboreoiulus pallidus*
Boreoiulus tenuis (Bigler)	
Nemasoma varicorne C. L. Koch	*Nemasoma varicorne*
Julus scandinavius Latzel	*Julus scandinavius*
Leptoiulus simplex glacialis (Verhoeff)	*Leptoiulus simplex glacialis*
Leptoiulus belgicus (Latzel)	
Leptoiulus bertkaui (Verhoeff)	
Allajulus nitidus (Verhoeff)	*Allajulus nitidus*
Cylindroiulus caeruleocinctus (Wood)	*Cylindroiulus caeruleocinctus*
Cylindroiulus latestriatus (Curtis)	
Cylindroiulus truncorum (Silvestri)	
Cylindroiulus punctatus (Leach)	*Cylindroiulus punctatus*
Brachyiulus pusillus (Leach)	*Brachyiulus pusillus*
Ommatoiulus rutilans (C. L. Koch)	*Ommatoiulus rutilans*
Ommatoiulus sabulosus (Linné)	*Ommatoiulus sabulosus*
Tachypodoiulus niger (Leach)	*Tachypodoiulus niger*
Craspedosoma alemannicum Verhoeff	*Craspedosoma rawlinsi* Leach
Craspedosoma simile Verhoeff	
Melogona gallica (Latzel)	*Melogona gallica*
Chordeuma silvestre C. L. Koch	*Chordeuma sylvestre*
Mycogona germanicum (Verhoeff)	*Mycogona germanicum*
	Orthochordeumella pallida (Rothenbühler)
Oxidus gracilis (C. L. Koch)	
Stosatea italica (Latzel)	
Brachydesmus superus Latzel	*Brachydesmus superus*
Polydesmus angustus Latzel	*Polydesmus angustus*
Polydesmus denticulatus C. L. Koch	*Polydesmus denticulatus*
Polydesmus inconstans Latzel	*Polydesmus inconstans*
Polydesmus testaceus C. L. Koch	*Polydesmus testaceus*

COMPARISON OF HOFFMANN'S DATA AND RECENT DATA

In the last ten years 23 of HOFFMANN's 36 listed species have been found again. With regard to this it is important to remember that nearly all the recent collecting has been achieved by pitfall trapping, and this probably accounts for the relatively low number of species found lately, in particular the blaniulids, some of which hardly ever fall into pitfall traps because of their hypogeal mode of life. Other species hardly ever or never taken in pitfall traps include *Polyxenus lagurus*, recorded by HOFFMANN, and the polydesmid, *Macrosternodesmus palicola*, as well as the glomerid, *Stygioglomeris crinita*, neither of which has been recorded at all from the Grand Duchy, and both of which are likely to occur in the calcareous areas. A discussion about the efficiency of pitfall traps in catching different species of millipedes is to be found in BRANQUART *et al.* (1995 and this volume). The other species found by HOFFMANN that have not been recorded recently are on the whole synanthropic or at the extreme limit of their geographical range. *Leptoiulus bertkaui* deserves special mention; HOFFMANN recorded it with reservations: he did find males on one occasion but could not find the species again. As the site

Source : MNHN, Paris

where he located it is in the drainage basin of the Rhine, it would not be particularly unexpected to find it.

HOFFMANN recorded *Craspedosoma rawlinsi* as two species, *Craspedosoma simile* and *C. alemannicum*, both described by VERHOEFF. This paper follows SPELDA (1991) in regarding them as subspecies at best. The gonopods are variable and it seems certain that we are looking at speciation in progress.

One species new to Luxemburg has been recorded. Seven adults of *Orthochordeumella pallida* were found at Weicherdange in the North.

Thus, in the light of present taxonomy, the list of species recorded in the Grand Duchy still stands at 36, though it will no doubt be added to in the future.

REGIONAL VARIATION IN SPECIES DISTRIBUTION

The northern part of the Grand Duchy is known as the Oesling, a dissected palaeozoic massif of Devonian age continuous with the Ardenne in Belgium and across the valley of the River Our which forms the frontier, with the Eifel in Germany. The plateau rises to about 550m above sea level, and the valleys are quite deep. The parent rocks are chiefly metamorphic schists and the soils tend to be mull-moder or moder brown earths, much of this area remaining forested. There are some small patches of limestone in this region.

The larger southern part of the country is called the Gutland and geologically belongs to the Secondary period. Lower-lying rocks shelve down to the Lorraine Plateau; these are Bunter sandstones, Muschelkalk, Keuper sandstones and Keuper marls of the Triassic, and Liassic sands and clays of the Jurassic period. While the Oesling tends to have oligotrophic acidic soils, the Gutland has rather warmer sands and extensive calcareous soils forming mulls in forests. But much of this land is cultivated and there are vines in the valley of the Moselle.

In the light of these observations, regional variations in species distributions are to be expected. Table 2 shows species that were found to be present in some stations in four different zones. The stations were sampled continuously from the end of the winter until the autumn by means of barber traps, which were emptied regularly, roughly every three weeks. Species lists for all the stations are likely to be incomplete at present, since only the one method of collecting was employed.

Most julids are liable to fall into pitfall traps, however, and relatively very few did so in the Oesling, which was dominated by polydesmids and glomerids in the traps, but which contains large populations of chordeumatids, active in the winter when the traps were not operational. Several species caught in the South were not caught in the Oesling; these include *Cylindroiulus caeruleocinctus, C. punctatus, Ommatoiulus sabulosus, O. rutilans, Melogona gallica* and *Polydesmus testaceus*. They are less common and some of them may be absent from the North, especially *O. rutilans*, which is at its northern limit in Luxembourg, although it penetrates the Ardenne massif in Belgium along the valley of the Meuse. The Gutland traps caught mainly julids which attained maximum numbers in the meso-xerothermic calcareous grasslands of the Keuper Marl.

Table 3 shows the numbers of julids caught in 22 of the sites where Barber traps were set from March/April until October. The numbers as they stand are not reliable for all quantitative calculations because the number of operational traps was not always the same on each site, some of the traps were damaged and specimens either lost or not caught, and the captures are from different years. They do nevertheless indicate some important qualitative trends and relative numbers of species on any one site, as pitfall trapping studies use to do (see GEOFFROY & CÉLÉRIER, this volume). The first 15 sites were sampled simultaneously by placing a series of traps from 4 metres on one side of a hedge to 4 metres on the other side. Thus there were four traps, one metre apart, at right angles to the hedge in the fields on either side, and there were

Source : MNHN, Paris

another four traps in the hedge itself. The traps in the hedge caught most of the millipedes. The last seven sites in Table 3 were more or less open calcareous grassland.

The results of the trapping lend further support to the view that the larger and longer-lived iteroparous species such as the julids shown in Table 3 are abundant in open habitats, see e.g. DUNGER & STEINMETZGER (1981), KIME (1992).

The open Keuper sites were dry in the summertime and a lot of large julids were caught in them. O'NEILL (1969) subjected seven species of millipede to desiccation and found that they differed significantly in their resistance to this stress; he attributed this to two factors, size and cuticular structure. He concluded from observations in the forests of Illinois that tolerant species are more numerous because of increased ability to disperse to new locations during unfavourable periods. These tolerant species were the larger : the numerous larger julids in Luxembourg, some of which are known to be thermophilous in summer, might well exemplify his argument.

TABLE 2. — Millipedes recorded in Barber traps in different regions of the Grand Duchy of Luxemburg. Cc = *Cylindroiulus caeruleocinctus*; Tn = *Tachypodoiulus niger*; Os = *Ommatoiulus sabulosus*; Or = *Ommatoiulus rutilans*; An = *Allajulus nitidus*; Js = *Julus scandinavius*; Cp= *Cylindroiulus punctatus*; Bp = *Brachyiulus pusillus*; Ls, Lsg = *Leptoiulus simplex glacialis*; Ap = *Archiboreoiulus pallidus*; Mg = *Melogona gallica*; Op = *Orthochordeumella pallida*; Cs = *Chordeuma silvestre*; Csp = *Craspedosoma* sp.; Gm = *Glomeris marginata*; Gh = *Glomeris hexasticha intermedia*; Pa = *Polydesmus angustus*; Pt = *Polydesmus testaceus*; Pd = *Polydesmus denticulatus*; Pi = *Polydesmus inconstans*; Bs = *Brachydesmus superus*.

SITE	MILLIPEDES RECORDED																						
	Cc	Tn	Os	Or	An	Js	Cp	Bp	Lsg	Ap	Mg	Op	Cs	Csp	Gm	Gh	Pa	Pt	Pd	Pi	Bs
OESLING: DEVONIAN																					
Bauschelterbierg						+									+		+		+		+
Beim Weier															+	+	+		+		+
Wanterheck																+	+		+		
Hartschlaegden		+												+			+				
Gresbourg		+								+				+	+	+					
Weicherdange												+		+	+	+	+		+		
Sauerwisen																	+		+		
GUTLAND: LIAS																					
Happfeldchen	+	+			+												+	+	+		
Hanner Weller	+	+			+												+				
Eiselsbierg	+	+													+						
Aucheler	+	+			+						+				+			+	+		+
Ehlerange						+		+													
Schuller	+				+																
Mondercange																		+			
GUTLAND: MUSCHELKALK																					
Rampelsbierg	+	+					+			+	+				+				+		+
Froumbierg		+	+				+		+		+							+	+		+
Tueschaker	+	+			+						+				+		+	+	+		+
Haerebierg		+													+						
GUTLAND: KEUPER																					
Rennpad	+	+	+			+															
Doulen	+	+	+	+		+					+							+			
Groebierg	+	+	+								+				+			+	+		
Sonnebierg	+	+	+		+	+					+		+		+	+		+	+		+
Aarnest	+	+	+		+	+					+				+			+		+	
Hunsdorf	+	+			+	+					+				+	+	+		+		
Kleibierg		+	+		+	+					+				+	+	+	+	+		+
Dennebierg	+	+	+	+	+	+												+			

Source : MNHN, Paris

TABLE 3. — Numbers of julids caught in pitfall traps. Species as in table 2; TOT = total number of julids per site. For species, see Table 2.

	Year	Soil type	Habitat Site description	Numbers of julids								
				Cc	Tn	Ls	Os	Or	An	Js	Cp	TOT
DEVONIAN												
Surre, Beim Weier	1989	Loam on schist	Hedge in grassland	-	-	-	-	-	-	-	-	0
Surre, Wanterheck	1989	Loam on schist	Hedge in grassland	-	-	-	-	-	-	-	-	0
Bavigne 1	1989	Loam on schist	Hedge in grassland	-	3	-	-	-	-	-	-	3
Bavigne, Gresler	1989	Loam on schist	Hedge in grassland	-	4	-	-	-	-	-	-	4
LIAS												
Clemency 1	1989	Clay	Hedge in grassland	1	27	-	-	-	1	-	-	29
Garnich	1989	Clay	Grass/hedge/arable	2	1	-	-	-	3	-	-	6
Kahler	1989	Clay	Hedge in grassland	1	6	-	-	-	-	-	-	7
Clemency 2	1989	Calcareous clay	Hedge in arable land	2	181	-	-	-	4	-	-	187
Boursdorf	1989	Calcareous loam	Grass/hedge/arable	14	240	-	-	-	-	-	1	255
Machtum	1989	Calcareous loam	Hedge in arable land	-	70	1	1	-	-	-	1	73
Oberdonven	1989	Calcareous loam	Hedge in grassland	4	123	-	-	-	2	-	-	129
Gostingen	1989	Calcareous loam	Hedge in arable land	-	34	-	-	-	-	-	-	34
KEUPER												
Junglinster, Rennpad	1989	Heavy clay	Hedge in grassland	22	1	-	2	-	-	5	-	30
Junglinster, Doulen	1989	Calc. colluvium	Hedge in grassland	168	189	-	6	1	-	2	-	366
Junglinster, Groebierg	1989	Leached loam	Hedge in grassland	30	110	-	3	-	-	-	-	143
Bech, Geyersknapp	1989	Calcareous clay	Grassland with juniper	102	8	-	2	156	-	18	-	286
Junglinster, Weimericht	1989	Calcareous clay	Grassland with bushes	133	144	-	155	87	2	4	-	525
Godbrange, Schleidelbierg	1989	Calcareous clay	Grassland	194	-	-	138	82	-	28	-	442
Altlinster, Dennebierg	1990	Calcareous clay	Grassland	315	1	-	99	13	6	59	-	493
Reckange, Billknapp	1990	Calcareous clay	Pasture & set-aside	299	18	-	18	-	-	9	-	344
Walferdange, Sonnebierg	1990	Calcareous clay	Grassland	278	116	-	11	-	37	45	-	487
Oberanven, Aarnescht	1991	Calcareous clay	Grassland/few pines	234	7		130	-	19	24	-	414

CRAWFORD (1979) noted that millipedes that live in deserts are usually large giving them more resistance to loss of water. Furthermore, REMMERT (1981) studied body size of terrestrial arthropods in relation to the abiotic parameters of their milieu, and concluded that for spiders and winged insects at least, the average body size, and the numbers of animals were governed by the relative humidity of the biotope.

The results from Luxemburg may reinforce these views strongly by statistically demonstrating the same phenomenon in Diplopoda. With regard to particular species and the environmental factors temperature and relative humidity, there is also accordance between these results in Luxemburg and the detailed works of PERTTUNEN (1953), BARLOW (1957), HAACKER (1968) and PEDROLI-CHRISTEN (1977, 1993) for *Julus scandinavius*, *Ommatoiulus*

Source : MNHN, Paris

sabulosus, O. rutilans and *Tachypodoiulus niger* in particular, which feature considerably in this study. Equally indicative is the absence, or near absence, of other species for which the parameters have been studied and which require more humid or stable environments to be found in closed forests. The most abundant millipede in the traps, *Cylindroiulus caeruleocinctus*, is described as hygrophile by HAACKER. Yet in Belgium, Luxemburg and Switzerland quantitative results indicate that it is largely found in open habitats, with peak numbers occurring in the spring. According to HAACKER, it may burrow in dry weather: a smaller peak is reported by PEDROLI-CHRISTEN in the autumn. HAACKER and later BLOWER (1985) have also correlated the presence of *C. caeruleocinctus* with a high pH value: the Luxemburg figures support this too. However, *C. caeruleocinctus* occurs in open woods on acidic sandstone soils in S. E.England, where the rainfall is relatively low, and where there are very few chordeumatids, and so it is possible that this reflects its tolerance of dry environments, and that its abundance on calcareous soils does the same. The same is true of *Allajulus nitidus*, which is common on calcic mulls, yet occurs on sandstone. It is considered to be hygrophile too (HAACKER, 1968), and burrows during the summer as well (GEOFFROY, 1981). The largest Western European julid, *Cylindroiulus londinensis*, not found in Luxemburg, is another case in point.

The dominance of julids in periodically dry environments may be due to their resistance to desiccation and/or their ability to burrow. The humid forests tend to be dominated by rapid-breeding semelparous species, reflecting their potential mathematical advantage in favourable conditions.

PHENOLOGY

Since the traps were set from March or April until October, and caught mainly adults, the numbers of chordeumatids recorded were disproportionately small. Adult *Orthochordeumella pallida* were trapped at Weicherdange between the middle of March and the beginning of May, 1989, the last one obtained was in a trap set on April 13. They occurred again in traps set from September 16 until October 6, and from October 6 until October 27, when operations ceased. At Clemency, 10 *Melogona gallica* (9 males, 1 female) were caught before April 25, 6 more males between then and May 29, and a last male between May 29 and June 19. No more were obtained before operations ceased on October 2. Results were similar in all the other sites where *M. gallica* was found. There was a remarkable preponderance of males. *Chordeuma silvestre* was also obtained in the spring on the Sonnebierg; adults of this species were captured by hand in two forests on October 17, 1982. On the same day *Craspedosoma rawlinsi/alemannicum* was similarly taken by hand in three forests. In the pitfalls traps, 26 segment specimens were caught in August, 28 segment specimens in September, and 28 segment specimens were caught by hand on October 12, 1991.

Looking at the polydesmids, adult *Polydesmus angustus* and *P. testaceus* were found in every month of trapping. *P. testaceus*, common in the South, appears to have a spring peak at least in a number of sites, but more results will be obtained and subject to analysis. *P. denticulatus* shows spring and summer activity in the Oesling, and a marked burst of summer activity in the South, where mainly wandering males were trapped during the warmest period of the year in dry calcareous grassland sites with the highest summer temperatures in the country. This was rather unexpected since *P. denticulatus* has a distinctly northern distribution in Europe and has generally been associated with sites where the water table is close to or at the surface of the soil, e.g. the polders (JEEKEL, 1978) and even in submerged sites (ZULKA, 1992). The species is described as eurytopic by several authors; it is however a fairly small polydesmid. There may be further support here for O'NEILL's observation that stressed millipedes wander, and we may be looking at migratory and/or sexual behaviour as well. In territory where there is a mosaic of wooded and non-wooded country, it is a little difficult to separate the resident species

Source : MNHN, Paris

from the wanderers by using Barber traps. This is why there will be some Berlese-Tullgren extractions made in this part of Luxemburg in the near future.

On the whole, julids and glomerids were found throughout the trapping period. There was certainly an early spring peak for the abundant *C. caeruleocinctus.*

In recent years *J. scandinavius* has been taken in a large number of pitfall traps in heathland and grassland; its numbers on the calcareous Keuper Marl are interesting: pitfall traps in calcareous woodland in Belgium have not caught it, yet it is widespread on neutral and acidic soils, both in woodland and open sites. PEDROLI-CHRISTEN (1993) reports its absence from forests on calcareous rocks in Switzerland.

ACKNOWLEDGEMENTS

I give my thanks to Professor Norbert STOMP, Director of the National Museum of Natural History in Luxemburg, and I owe a special debt of gratitude to Marc MEYER, who provided me with all the millipedes found in the pitfall trapping schemes intended primarily to monitor beetle populations. Not only that, Dr. MEYER furnished information about the sites, discussed the ecology of the regions with me and read through the manuscript.

REFERENCES

BARLOW, C. A. , 1957. — A factorial analysis of distribution in three species of Diplopoda. *Tijds. Ent.*, **100** : 349-426.

BLOWER, J. G., 1985. — *Millipedes (Synopses of the Br. Fauna* NS, **35**). London, E. J. Brill & W. Backhuys, 242 pp.

BRANQUART, E., KIME, R. D., DUFRENE, M. & WAUTHY, G., 1995. — Macroarthropod-habitat relationships in oak forests in South Belgium. I. Environments and communities. *Pedobiologia*, **39** : 243-263.

CRAWFORD, C. S., 1979. — Desert millipedes: a rationale for their distribution. *In* : M. CAMATINI, *Myriapod Biology*. London, Acadademic Press : 171-181.

DUNGER, W. & STEINMETZGER, K., 1981. — Ökologische Untersuchungen an Diplopoden einer Rasen-Wald-Catena im Thuringer Kalkgebiet. *Zool. Jb. Syst.* **108** : 519-553.

GEOFFROY, J. J., 1981. — Modalité de la coexistence de deux diplopodes, *Cylindroiulus punctatus* (Leach) et *Cylindroiulus nitidus* (Verhoeff) dans un écosystème forestier du Bassin Parisien. *Acta Oecol., Oecol. gener.*, **2** : 227-243.

HAACKER, U., 1968. — Deskriptive, experimentelle und vergleichende Untersuchungen zur Autökologie rhein-mainischer Diplopoden. *Oecologia* , **1** : 87-129.

JEEKEL, C. A. W., 1978. — Voorlopige atlas van de verspreiding der Nederlandse miljoenpoten (Diplopoda) Amsterdam : 1-68.

KIME, R. D., 1992. — On Abundance of West-European Millipedes (Diplopoda). *In*: : [E. MEYER, K. THALER & W. SCHEDL, *Advances in Myriapodology*.] *Ber. nat.-med. Verein Innsbruck*, **Suppl.10** : 393-399.

O'NEILL, R. V., 1969. — Comparative Desiccation Tolerance in Seven Species of Millipedes. *Am. Midl. Nat.*, **82** : 182-187.

PEDROLI-CHRISTEN, A., 1977. — Etude des Diplopodes dans une tourbière du Haut-Jura. *Bull. Soc. Neuchâtel Sci. nat.*, **104** : 21-34.

PEDROLI-CHRISTEN, A., 1993. — *Faunistique des Mille-pattes de Suisse (Diplopoda)*. Neuchâtel, Centre Suisse de Cartographie de la Faune : 1-167.

PERTTUNEN, V., 1953. — Reactions of Diplopods to the relative humidity of the air. *Ann. Zool. Soc. "Vanamo"*, **16** : 1-69.

REMMERT, H., 1981. — Body Size of Terrestrial Arthropods and Biomass of their Populations in Relation to the Abiotic Parameters of their Milieu. *Oecologia* , **50** : 12-13.

REMY, P. & HOFFMAN, J., 1959. — Faune des Myriapodes du Grand-Duché de Luxembourg. *Archives de la Section des Sciences de l'Institut Grand-Ducal*, **26** : 199-236.

SPELDA, J., 1991. — Zur Faunistik und Systematik der Tausendfüssler (Myriapoda) Sudwestdeutschlands. *Jh. Ges. Naturkde. Wurttemburg*, **146** : 211-232.

ZULKA, K. P., 1992. — Myriapods from a central European rivers floodplain. *In* : [E. MEYER, K. THALER & W. SCHEDL, *Advances in Myriapodology*.] *Ber. nat.-med.Verein Innsbruck*, **suppl. 10** : 189.

Source : MNHN, Paris

Source : MNHN, Paris

Some Patterns in the Distribution and Origin of the Lithobiomorph Centipede Fauna of the Russian Plain (Chilopoda: Lithobiomorpha)

Nadezhda T. ZALESSKAJA & Sergei I. GOLOVATCH

Institute for Problems of Ecology and Evolution,
Russian Academy of Sciences, Leninsky prospekt 33, 117071 Moscow (V-71), Russia

ABSTRACT

Based on the patterns of present-day landscape-zonal distribution, the lithobiomorph fauna of the Russian Plain (25 species or subspecies) appears to be ecologically and historically very strongly associated with a nemoral (= broadleaved forest) type of vegetation. This allows the reconstruction of the group's regional faunogenesis, with the fauna shown to be eventually fully migratory, derivative of the adjacent major (Carpathians/Moldova, Caucasus and/or Crimea) and minor (Urals) nemoral refuges. This corresponds closely to the patterns reported for numerous other animal groups.

RÉSUMÉ

Répartition et origine de la faune de chilopodes lithobiomorphes de la plaine russe (Chilopoda : Lithobiomorpha).

D'après les modalités actuelles de la répartition zonale des paysages, la faune de lithobiomorphes de la plaine russe, composée de 25 espèces ou sous-espèces, apparaît fortement associée, historiquement et écologiquement, à une formation végétale de type forêt de feuillus. Ceci permet de reconstruire la genèse régionale des groupes faunistiques, lesquels peuvent avoir entièrement migré, dérivant de refuges forestiers adjacents importants (Carpates/Moldavie, Caucase et/ou Crimée) ou mineurs (Oural). Ces modalités se rapprochent beaucoup de celles décrites pour de nombreux autres groupes d'animaux.

INTRODUCTION

The Russian Plain, a vast area covering most of the European part of the former Soviet Union, has long been known as displaying a classical latitudinal nature zonation combined with an increasing longitudinal continentality, presenting thereby a highly interesting and important arena for biogeographical studies. The belts/zones of tundra, taiga, mixed coniferous-deciduous forests, broadleaved forests, steppe, semidesert, and desert form a full and practically ideal succession from north to south (e.g. MILKOV, 1977). The problem of natural distributions in Lithobiomorpha is still open to discussion (e.g. EASON, 1974,1992), primarily due to the order's confused taxonomy (especially at the generic level) and our insufficient

ZALESSKAJA, N. T. & GOLOVATCH, S. I., 1996. — Some patterns in the distribution and origin of the lithobiomorph centipede fauna of the Russian Plain (Chilopoda: Lithobiomorpha). *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 265-268. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

collecting/identification efforts. Although the Russian Plain can boast to be perhaps the best explored region of the former USSR as regards the lithobiomorph fauna (ZALESSKAJA, 1978), it still remains an area where lots of centipede records are dubious, and some are even new to the regional list. Furthermore, general patterns of lithobiomorph chorology, let alone faunogenesis, on the Russian Plain have never been adequately discussed. This paper aims at filling in this gap at least partially, with consideration of all 25 lithobiomorph species or subspecies currently known to populate the region concerned. Much of new faunistic evidence derives from numerous localities covering the entire nemoral (= broadleaved forest) biome as part of a broader project on soil macrofauna communities of the Russian Plain (e.g. PENEV, 1992; ESJUNIN *et al.*, 1993). It appears as Contribution Nr. 8 to the project entitled "Spatial variation in soil macrofauna communities of East European oak forests in relation to environmental factors", conducted by L. D. PENEV and S. I. GOLOVATCH, sponsored by the USSR Academy of Sciences, Moscow. This project has enabled us to be considerably more precise in the distribution patterns and even enrich the list of Russian Plain lithobiomorphs, especially as regards the fauna of oak, mainly *Quercus robur* L., forests.

TABLE 1. — Distribution of lithobiomorph species on the Russian Plain. Symbols: DP - general distribution pattern; C - zonal-landscape distribution; H - Holarctic; P - Palearctic; E - (pan)-European; CE - central European; SE - South(east) European; EM - East Mediterranean; Ca - Caucasian; Si - Siberian; End - endemic; Z - natural vegetation zones; Tu - tundra; T - taiga; F - mixed broadleaved-coniferous forests; FS - forest-steppe; S - steppe; Mt - mountainous lands south of the Russian Plain (Carpathians, Crimea and/or Caucasus).

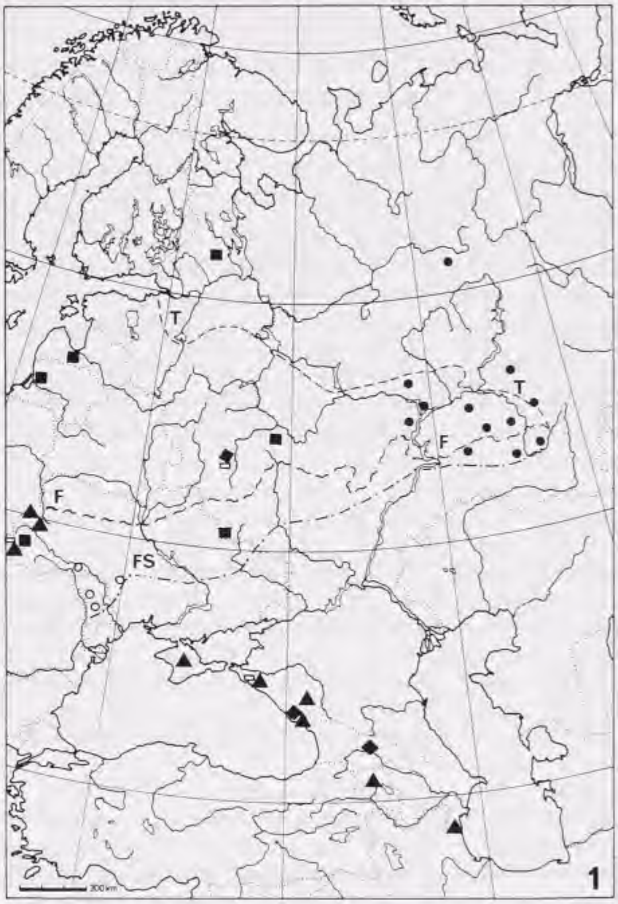
Lithobiomorph species		DP	
Nr	Taxa	C	Z
1	*Lamyctes fulvicornis* Meinert, 1868	H	T-S, Mt
2	*Lithobius forficatus* Linnaeus, 1758	H	F-Mt
3	*Monotarsobius curtipes* (C. Koch, 1847)	P	Tu-Mt
4	*M. crassipes* (L. Koch, 1862)	P	F-Mt
5	*Lithobius erythrocephalus* C. Koch, 1847	E	F-FS
6	*L. melanops* Newport, 1845	E	F-FS
7	*L. tenebrosus* Meinert, 1872 [= *L. nigrifrons* Latzel & Haase, 1880]	E	T-FS
8	*L. lucifugus* L. Koch, 1862	E	F-Mt
9	*L. piceus* L. Koch, 1862	E	FS-Mt
10	*Monotarsobius aeruginosus* (L. Koch, 1862)	E	FS-Mt
11	*L. microps* Meinert, 1868 [= *M. duboscqui* (Brölemann, 1896)]	E	FS
12	*Lithobius cyrtopus* Latzel, 1880	CE	FS
13	*L. borealis* Meinert, 1868 [= *L. lapidicola* A.A. (non Meinert)]	CE	FS
14	*L. pelidnus* Haase, 1880	CE	F-Mt
15	*L. validus* Meinert, 1872	CE	FS
16	*Monotarsobius microps* (A.A. non Meinert)	CE	FS
17	*M. sseliwanoffi* (Garbowski, 1897)	SE	FS-Mt
18	*Lithobius mutabilis* L. Koch, 1862	SE	FS
19	*L. parietum* Verhoeff, 1899	SE	FS
20	*L. viriatus* Sseliwanoff, 1880	EM	FS-Mt
21	*L. cronebergii* Sseliwanoff, 1880	Ca	F, Mt
22	*L. proximus* Sseliwanoff, 1878	Si	T-S
23	*L. lusitanus tataricus* Folkmanova & Dobroruka, 1960	End	FS
24	*Eupolybothrus verrucosus* (Sseliwanoff, 1876)	End	FS
25	*Hessebius multicalcaratus* Dobroruka, 1958	End	S

DISTRIBUTION OF LITHOBIOMORPHA ON THE RUSSIAN PLAIN

Table 1 shows the patterns of distribution of the Russian Plain lithobiomorph species, some examples are also presented in maps (Figs 1-2). As one can see, the bulk of the fauna is restricted to the zones of mixed broadleaved-coniferous forests and forest-steppe, while both to the north (taiga and tundra) and south (steppe) the distribution becomes increasingly sporadic

Source : MNHN, Paris

and more closely associated with intrazonal, often anthropogenic, habitats. A similar pattern is observed from west to east, with gradual impoverishment of the fauna from both Moldova and the Carpathians toward the Urals. Thus, the Dniester seems to serve as the easternmost limit in the distributions of *Eupolybothrus verrucosus*, *Lithobius microps, Lithobius cyrtopus, L. viriatus, L. piceus*, the Bug River "stops" also *L. parietum*, the Seversky Doniets also *Monotarsobius aeruginosus* and *L. microps* as well as most of *M. crassipes*, the Don both *Lithobius erythrocephalus* and perhaps also *L. pelidnus* (Figs 1-2). The Volga flow seems to delimit the distributions of *L. lucifugus*, *L. melanops*, and *L. forficatus* from the west, and *L. proximus* from the east (Figs 1-2). The Urals appear to support the poorest fauna, i.e. the extremely widespread, Holarctic *Monotarsobius curtipes* as well as the Siberian *Lithobius proximus*.



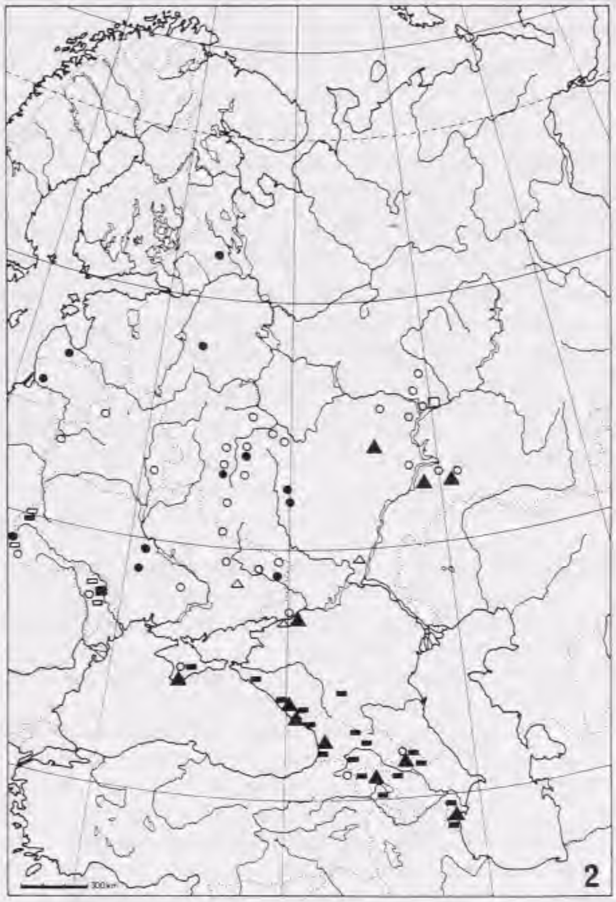


FIG. 1. — Distribution of some *Lithobius* species on the Russian Plain and in adjacent mountainous lands: filled diamond: *L. cronebergii* - filled square: *L. melanops* - open circle: *L. parietum* - open quadrangle: *L. pelidnus* - filled triangle: *L. piceus* - filled circle: *L. proximus*. T: southern border of the taiga belt; F: southern border of the nemoral forest belt; FS: southern border of the forest-steppe belt.

FIG. 2. — Distribution of some Lithobiomorpha on the Russian Plain and in adjacent mountainous lands: filled square: *Eupolybothrus verrucosus* - open triangle: *Hessebius multicalcaratus* - open quadrangle: *Lithobius cyrtopus* - open circle: *L. lucifugus* - open square: *L. lusitanus tataricus* - filled circle: *L. tenebrosus* - filled quadrangle: *L. viriatus* - filled triangle: *Monotarsobius sseliwanoffi*.

Source : MNHN, Paris

FAUNOGENESIS

The above trends both in the preponderance of Russian Plain Lithobiomorpha to the nemoral biome and in a west-east faunal impoverishment can be accounted for in terms of both present-day ecological preferences of the group concerned and historical reasons.

As in the case of millipedes, the lithobiomorph fauna of the Russian Plain appears to be eventually fully migratory in origin. The role of the adjacent major nemoral refuges is certainly a leading one in the fauna's conservation and restoration during Pleistocene glaciations and interglacials (including the Holocene), respectively. It is not by chance that nearly all Lithobiomorpha populating the Russian Plain occur also in the Caucasus, Crimea and/or Carpathians with the adjacent Moldova (see Table 1). This is particularly evident when both *Lithobius cronebergii* and *Monotarsobius sseliwanoffi* are taken as examples (Figs 1-2). The former species had been believed to be confined to the Caucasus Major (ZALESSKAJA, 1978) until it was discovered in the southern part of the Kaluga Area in 1991. Similarly, *M. sseliwanoffi* occurs throughout the Caucasus and Crimea, with only a few records in the lower Don and middle Volga flows involved. The role of a southern Ural refuge is clearly subordinate, being probably best expressed only as regards *Lithobius proximus*. The present-day distributions, but not necessarily origins, of Russian Plain endemic lithobiomorphs seem to have been associated with spreading from the Carpathians/Moldova (*Eupolybothrus verrucosus*), ?Urals (*Lithobius lusitanus tataricus*, a dubious form whose status requires a revision), and Caucasus/Crimea (*Hessebius multicalcaratus*). Anthropochores must have attained their vast distributions very recently, during the last few decades/centuries. This can be suggested at least for *Lithobius forficatus* and *Monotarsobius curtipes* known to very often occur in purely synanthropic habitats. The above patterns correspond very closely to the faunogenetic reconstructions recently conducted for Russian Plain soil/litter-dwelling spiders (Araneae) (ESJUNIN *et al.*, 1993), millipedes (Diplopoda) (GOLOVATCH, 1992), and earthworms (Lumbricidae) (VASILEV, 1993). In other words, lithobiomorph centipedes join the numerous other soil/litter macrofauna (and also some mammal, bird, insect, etc.) groups on the Russian Plain proved to be both ecologically and historically very strongly associated with a nemoral type of vegetation.

REFERENCES

EASON, E. H., 1974. — The type specimens and identity of species described in the genus *Lithobius* by F. Meinert. *Zool. J. Linn. Soc.*, **55** : 1-52.

EASON, E. H., 1992. — On the taxonomy and geographical distribution of the Lithobiomorpha. *Ber. nat.-med. Verein Innsbruck*, **suppl. 10** : 1-9.

ESJUNIN, S. L., GOLOVATCH, S. I. & PENEV L. D., 1993. — The fauna and zoogeography of spiders (Arachnida: Araneae) inhabiting oak forests of the East European Plain. *Ber. nat.-med. Verein Innsbruck*, **80** : 179-249.

GOLOVATCH, S. I., 1992. — Some patterns in the distribution and origin of the millipede fauna of the Russian Plain (Diplopoda). *Ber. nat.-med. Verein Innsbruck*, **suppl. 10** : 373-383.

MILKOV, F. N., 1977. — *Nature Zones of the USSR*. Moscow, "Mysl" Publ., 295 pp. (in Russian).

PENEV, L. D., 1992. — Qualitative and quantitative spatial variation in soil wire-worm assemblages in relation to climatic and habitat factors. *Oikos*, **63**: 180-192.

VASILEV, A. I., 1993. — Some particulars in the distribution and faunogenesis of earthworms in oak forests of the Russian Plain (Oligochaeta, Lumbricina, Lumbricidae). *Doklady Ross. Akad. nauk*, **332** (5) : 657-659 (in Russian).

ZALESSKAJA, N. T., 1978. — *Identification Book of Lithobiomorph Centipedes of the USSR*. Moscow, "Nauka" Publ., 212 pp. (in Russian).

Source : MNHN, Paris

The French Millipede Survey: Towards a Comprehensive Inventory and Cartography of the Diplopoda in France

Jean-Jacques ***GEOFFROY***

CNRS, Muséum National d'Histoire Naturelle, Laboratoire d'Ecologie Générale
4, avenue du Petit Château, F-91800 Brunoy, France

ABSTRACT

During recent years, field investigations have been carried out in the edaphic compartments of various ecosystem types (forests, meadows, deep cave and high mountain biotopes, anthropogenic and suburban sites) providing new zoogeographical data that have to be added to recent overviews dealing with the millipede check-list and distribution in France. 18 millipede species have been newly recorded from France during the period 1980-1995. This brings the total number of species to 282 for all millipede taxa (most subspecies are not taken in account). Recent trends in zoogeographical studies in Europe show that millipede biodiversity studies, monitoring, mapping, and the preservation of special sites will be of interest for the future. Among the 8 millipede orders present in France, *Chordeumatida / Craspedosomatida* is the dominant one, representing >40% of the specific and generic richness. This seem to be a result of a wide range of origins related to Atlantic, north continental, alpine, Mediterranean and Pyrenean components, some of them characterized by a high degree of endemism. The first cartographic exercise that has been initiated is a provisional Atlas based on the administrative boundaries of the 95 French "Départements". This atlas is up to date for the orders Polyxenida, Glomerida, Polyzoniida, Platydesmida and Callipodida; work is continuing on the orders Chordeumatida, Polydesmida and Julida. Based on research carried out by EIS, maps of millipede distribution are being drawn up, following the 10 km x 10 km UTM grid format. This step of the work is still in its early stages, because of the need to verify much of the previous data. Future initiatives will be developed towards four main aims: (i) Permanent updating of the check-list of species according to recent knowledge in millipede systematics and nomenclature. (ii) Permanent updating of the "Provisional Departmental Atlas" of species. (iii) Progressive updating of the UTM distribution maps. (iv) Proposals for precise recording of the zoogeographical distribution of species according to cartographic methods developed by the *Service du Patrimoine Naturel* (IEGB, MNHN, Paris). A FAUNA GALLICA DIPLOPODA file is proposed.

RÉSUMÉ

La faune des diplopodes de France : étapes vers un inventaire complet et un atlas de répartition géographique des espèces.

Les récentes recherches menées dans les compartiments édaphiques de divers écosystèmes portent à 282 le nombre total d'espèces de diplopodes répertoriées en France. Elles se répartissent au sein de 98 genres. 19 d'entre elles ont été décrites ou inventoriées entre 1980 et 1995, ce qui traduit une augmentation de 6,7% de la richesse spécifique connue au cours de cette période. Les espèces de France appartiennent aux huit ordres européens (sur les 16 ordres et sous-ordres qui composent la classe DIPLOPODA) : Polyxenida, Glomerida, Polyzoniida, Platydesmida, Callipodida, Craspedosomatida,

GEOFFROY, J.-J., 1996. — The french millipede survey: towards a comprehensive inventory and cartography of the Diplopoda in France. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 269-280. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

Polydesmida & Julida. La mise en forme des données les plus récentes confirme la large dominance de l'ordre Chordeumatida qui représente 40% de la richesse tant spécifique que générique. Cela s'explique par l'origine des espèces représentées par des composantes biogéographiques variées et caractérisées parfois par un très fort endémisme. Basé sur le critère de présence-absence à l'intérieur des limites administratives départementales, la réalisation d'un atlas est destinée à produire un document à partir duquel une cartographie en rapport avec les limites biogéographiques naturelles sera facilitée. Il est à jour pour les ordres Polyxenida, Glomerida, Polyzoniida, Platydesmida, & Callipodida et en cours d'aménagement pour les ordres Chordeumatida, Polydesmida & Julida. Une cartographie basée sur la grille des carrés UTM 10 km x 10 km, faite en coordination avec les travaux européens de l'EIS paraît, à terme, comme une contribution à l'enrichissement de FAUNA EUROPAEA EVERTEBRATA (banque de données faunistique européenne). La précision apportée par les carrés de 10 km x 10 km paraît largement suffisante pour une étude à l'échelle nationale. Les bases de données mises en oeuvre doivent être précises mais demeurer claires et pratiques. Il convient donc de ne considérer qu'un nombre restreint de types d'espèces ou d'écosystèmes de référence. On considère d'une part les espèces à large répartition, d'autre part les espèces liées soit aux influences méditerranéennes, atlantiques ou septentrionales, soit à des milieux particuliers : cavernicoles, nivicoles ou halophiles. Conformément à une proposition du Conseil de l'Europe, la France est découpée en 5 régions biogéographiques : atlantique, continentale, méditerranéenne, alpine & pyrénéenne. En dépit de son caractère arbitraire, ce découpage peut contribuer à l'étude de la biodiversité de faunes naturelles. De plus, nombre d'espèces chevauchant deux ou plusieurs zones, celles-ci pourront être comparées à l'aide d'indices de similitude. Dans un souci de simplification, l'appartenance des espèces à divers environnements est limitée à 5 types d'écosystèmes : écosystèmes de plaines, côtiers, d'altitude (hauts-plateaux & montagnes), insulaires, souterrains. *FAUNA GALLICA DIPLOPODA* est une base de données destinée à gérer la répartition et la biodiversité des diplopodes de France. Elle est élaborée dans 4è Dimension sur système MacIntosh et met en relation 14 fichiers de données constitués autour du catalogue des espèces. Les fichiers principaux concernent les localités et les collectes. Le code-localité désigne la commune et un ensemble de paramètres précisant sa situation et les caractéristiques de l'environnement. Les coordonnées géographiques autorisent un transfert des données vers des systèmes de cartographie automatique traités par divers organismes. Un outil de cette nature facilite, à terme, la mise à jour de l'inventaire des espèces en fonction de l'avancée des recherches en systématique et en nomenclature, de même que la mise en forme de l'atlas départemental. L'essentiel des informations provient à ce jour de données issues de collections de référence (MNHN, Paris) ou de bases bibliographiques (Centre International de Myriapodologie, BiblioMac-Milpat). Il convient alors de mettre ces informations en relation avec les capacités de traitement d'organismes tels que le Secrétariat Faune-Flore du MNHN et de faciliter la constitution d'un réseau d'observateurs-collecteurs capables, en liaison permanente avec des chercheurs spécialistes, de multiplier les points d'observation sur le territoire considéré.

INTRODUCTION

The growing interest in biodiversity has prompted many authors to consider the question of the number of species there are likely to be on Earth (see LÉVÊQUE, 1994; SOLBRIG, van EMDEN & van OORDT, 1992; WILSON, 1993). Some papers describe steps towards an estimate of the number of species either from a global assumption (MAY, 1992) or in connection with particular taxa, area, environment or even locality (JUBERTHIE & DECU, 1994; SERRA-COBO *et al.*, 1993).

Dealing with terrestrial invertebrates, there is obviously no group of organisms for which the total number of species is known directly and certainly no group of arthropods for which even a majority of species are known or described. The inventory of living forms is still very far from complete, even in taxa usually considered as well-known. To this reality of which we are reminded by BARBAULT (1994) has to be added the fact that such an inventory is still not achieved in regions or countries usually considered as well-worked. Most arguments about global biodiversity depend on a series of assumptions about the connection between local species diversity and regional (or "national") diversity (see CULVER & HOLSINGER, 1992; ERWIN, 1988).

Looking at this situation face to face, and so far as the specific richness and scarcity of species are good criteria for evaluating ecological systems (BLANDIN, 1989), we must emphasize the importance of precise and comprehensive species inventories and taxonomical diversity studies, wherever it is possible -notably in West-European areas- as preliminary geographical tools for further analysis of biodiversity (MAURER, 1994). We describe below the evolution of a FRENCH MILLIPEDE SURVEY, from the initial check-list of species to a computer data-base to serve as a tool for future biodiversity studies on Diplopoda in France.

Source : MNHN, Paris

RESULTS

Check-list of the millipede species

During last few years, field investigations have been carried out in the edaphic compartments of various ecosystem types (forests, meadows, deep cave and high mountain biotopes, anthropogenic and suburban sites, etc.), providing new zoogeographical data (see GEOFFROY, 1981) to be added to recent reviews dealing with millipede check-lists and distribution in France. Thus, 20 millipede species have been newly recorded on French territory during the 1980-1995 period (Table 1). This allow us to conclude that the total number of species is at present 282 for all millipede taxa (most of subspecies are not taken in account). Some of these taxa have to be added to the previous check-list proposed by GEOFFROY (1990a).

Table 1. — Millepede species discovered or described in France during the 1980-1995 period. Data from GEOFFROY, 1990b and GEOFFROY & MAURIÈS, 1992. Original data from GEOFFROY, MAURIÈS, KIME & PEDROLI-CHRISTEN.

Species	Distribution ("département")	Environment
Trachysphaera drescoi (Condé & Demange, 1961)	Pyrénées-Atlantiques	Caves
Brachychaeteuma bagnalli Verhœff, 1911	Rhône	Caves
Crossosoma mauriesi Strasser, 1970	Alpes-Maritimes	Soil & high mountain
Crossosoma cavernicola (Manfredi, 1951)	Alpes-Maritimes	Caves
Hispaniosoma racovitzai Ribaut, 1913	Ariège	Soil & high mountain
Opisthocheiron canayerensis Mauriès & Geoffroy, 1982	Gard	Caves
Origmatogona kimeorum Mauriès, 1990	Dordogne	Soil
Rhymogona cervina (Verhœff, 1910)	Doubs (new for France!)	Soil
Rhymogona montivaga (Verhœff, 1894)	Explanation in the text	Soil & Caves
Vascosoma coiffaiti Mauriès, 1966	Pyrénées-Atlantiques	Caves
Vascosoma coiffaiti falsaforma Mauriès, 1990	Pyrénées-Atlantiques	Caves
Vascosoma duprei Mauriès, 1990	Pyrénées-Atlantiques	Caves
Orthochordeumella leclerci Mauriès, 1986	Ardèche	Caves
Galliocookia leclerci Mauriès, 1983	Gard	Caves
Galliocookia balazuci Mauriès, 1983	Gard	Caves
Mastigonodesmus lopezi Mauriès, 1980	Hérault	Caves
Mastigonodesmus fagniezi Mauriès, 1982	Gard	Caves
Occitanocookia hirsuta Mauriès, 1980	Hérault	Caves
Archiboreoiulus pallidus (Brade-Birks, 1920)	Cher, Meurthe-et-Moselle, Ain	Caves
Dolichoiulus tongiorgii Strasser, 1973	Alpes-Maritimes, Gard	Halophilous

Rhymogona cervina (Verhœff, 1910), after revision of the collection in MNHN, Paris, is new for France (unpublished data, MAURIÈS & PEDROLI-CHRISTEN, pers. comm.). It is known from Les Gras (Doubs), a locality closely related to the contact zone with *Rhymogona montivaga* and the Swiss Jura.

Rhymogona montivaga (Verhœff, 1894) is new for the check-list of French millipedes, because of its synonymy with *Rhymogona silvatica* (Rothenbühler, 1899) and *R. s. hessei* (Ravoux, 1935). It is distributed in Côte d'Or, Isère, Haute-Marne, Rhône, Haute-Saône, Haute-Savoie.

A third nominal species, *Rhymogona alemannica* (Verhœff, 1910) is known from Meurthe-et-Moselle and Haut-Rhin.

Richness and biodiversity of millipede taxa

Recent zoogeographical trends in Europe show that invertebrate biodiversity studies, monitoring and mapping, and preservation of special sites are more and more of great interest for the future (GONSETH, 1993; MAURIN & GUILBOT, 1993; RASMONT, 1993). In connection with the EUROPEAN MILLIPEDE SURVEY (E.I.S.), KIME (1990) published a first provisional atlas of

Source : MNHN, Paris

European myriapods, closely linked to the work done by the BRITISH MYRIAPOD GROUP (1988; see BARBER & JONES, this volume).

Among the 8 millipede orders present in France (GEOFFROY, 1992, 1993a), Chordeumatida / Craspedosomatida is the most dominant one. It represents >40% of the specific and generic richness (113 species). This appears to be a result of the wide range of origins related to Atlantic, north continental, alpine, Mediterranean and Pyrenean components, some of them characterised by a very high degree of endemism (Table 2). This result is quite different in the British fauna, in which Chordeumatida (9 species) represent only 15.5% of the whole Diplopoda (after BLOWER, 1985). On the contrary, in Switzerland, the importance of the order Chordeumatida is relatively high, 33.9% for 43 species (after PEDROLI-CHRISTEN, 1993). In Italy, where we can see a high specific richness of millipedes, it represents 31.5% (148 species) of the Diplopoda (after STRASSER & MINELLI, 1984).

TABLE 2. — Taxonomic diversity of the Diplopoda in France. See for comparison GEOFFROY, 1989, 1990a, 1990b, 1993b; GEOFFROY & MAURIÈS, 1992.

Taxa (Orders & Sub-orders)	Species Richness		%	
Polyxenida		5		1.8
Glomerida		30		10.6
Polyzoniida		3		1.1
Platydesmida		1		0.4
Callipodida		3		1.1
Chordeumatida/Craspedosomatida		113		40.1
Craspedosomatidea	93		33.0	
Chordeumatidea	20		7.1	
Polydesmida		36		12.7
Julida		91		32.2
Blaniulidea	30		10.6	
Julidea	61		21.6	
Class Diplopoda		282		100.0

The comparison of the species richness of the Diplopoda in France with other European countries shows the possible mediterranean influence on these results related to some unnatural administrative limits (Table 3). It would be of great interest to complete this comparative review with more precise data from Scandinavia, Germany, Austria, Central Europe and Spain.

TABLE 3. — Compared specific richness of millipede fauna in different Western European countries.

Country	N species	Reference
Luxemburg (Gd Duchy)	36	REMY & HOFFMANN, 1959; KIME, this volume
Denmark	39	ENGHOFF, 1974
Netherlands	46	JEEKEL, 1978
U. K.	52	BLOWER, 1985
Switzerland	127	PEDROLI-CHRISTEN, 1993
Germany	160	SCHUBART, 1934
France	282	This work
Italy	470	STRASSER & MINELLI, 1984

Source : MNHN, Paris

Provisional departmental atlas

The first cartographic project that has started is a provisional Atlas using the administrative limits of the 95 French "départements", as initially used for the counties and vice-counties of the United Kingdom, (BLOWER, 1985). Based on a "presence-absence" criterion, this atlas will provide a basic document on biogeographic distribution. It is up to date for the orders Polyxenida, Glomerida, Polyzoniida, Platydesmida and Callipodida (unpublished data); work on the orders Chordeumatida/Craspedosomatida, Polydesmida and Julida is in progress (GEOFFROY, 1989, 1993b).

UTM grids maps of French millipedes

In accordance with research by EIS members (KIME, 1990), distribution maps of millipede species are in preparation, using the 10 km x 10 km UTM grid square. This step of the work is still at an early stage, because of the necessity to examine old records from the literature and museum collections and to correct their identification and bring nomenclature and classification up-to-date. This will be a contribution to the EIS FAUNA EUROPAEA EVERTEBRATA data base (GEOFFROY, 1994a, 1994b).

Fauna Gallica Diplopoda: a data base

FAUNA GALLICA DIPLOPODA is a data base whose aim is the management and monitoring of the distribution and biodiversity of millipedes in France. It is developped on "4th dimension" data base for Macintosh computers which allows 14 data files to be organized around the checklist of species. The main data files deal with localities and samples (Fig. 1). The main structure of the data-base is adapted from a previous one used by the GILIF Group for Lepidoptera (MOTHIRON, 1993).

The locality file points out the commune, city-code, co-ordinates and several parameters dealing with precise situation and environment. The geographic co-ordinates (grades and UTM grid) allow data-transfer to automatic cartographic systems used in centralized institutes. It is the first file to be completed. Then, linked to the previous one, the collect-file gives information related on dates, collectors and lists of sampled species.

Such a data-base must be as precise and as complete as possible but, in order to be understandable to new workers (colleagues, other specialists, ...), it must be quite simple and clear. In order to avoid useless complexity, it seems advisable to select only a restricted number of species categories and ecosystem types.

— Species categories

On one hand, we have to consider species with a wide-range distribution; on the other hand, species closely related to either Mediterranean, Atlantic and northern influences, or special environments such as the halophile category, coastal (MAURIÈS, 1982), high mountain (GEOFFROY, 1981) and caves or any other deep subterranean biotope.

In regard to this, a provisional checklist of highly troglophitic and troglobitic French millipedes has been proposed (GEOFFROY, 1994a). It is composed of 34 species : 5 Glomerida, 14 Chordeumatida, 6 Polydesmida and 9 Julida. Among these species, 7 taxa can be considered as interesting ones for natural patrimony. They are of special interest either for biogeography or evolutionary and paleontological history of lineages and territories. These species and their habitat should be selected for conservation projects in order to maintain the biodiversity level of these groups on a national and European scale. These taxa occur in high limestones sites in the Alps (genus *Broelemanneuma*), the Pyrenees (genus *Vascoblaniulus*) and in the Cevennes ("Causse de Canayère et de Bramabiau"). It should be possible, in the future, to be able to distinguish other such interesting taxa among the French fauna.

Source : MNHN, Paris

At present, this selection contains the 7 following troglobitic species :

Broelemanneuma furcatum Ribaut 1913	ALPINE
Broelemanneuma gayi Demange 1968	ALPINE
Broelemanneuma gineti Ribaut 1954	ALPINE
Broelemanneuma palmatum (Brölemann 1902)	ALPINE
Broelemanneuma pectiniger (Brölemann 1902)	ALPINE
Opisthocheiron canayerensis Mauriès & Geoffroy 1982	MEDITERRANEAN
Vascoblaniulus cabidochei Mauriès 1967	PYRENEAN

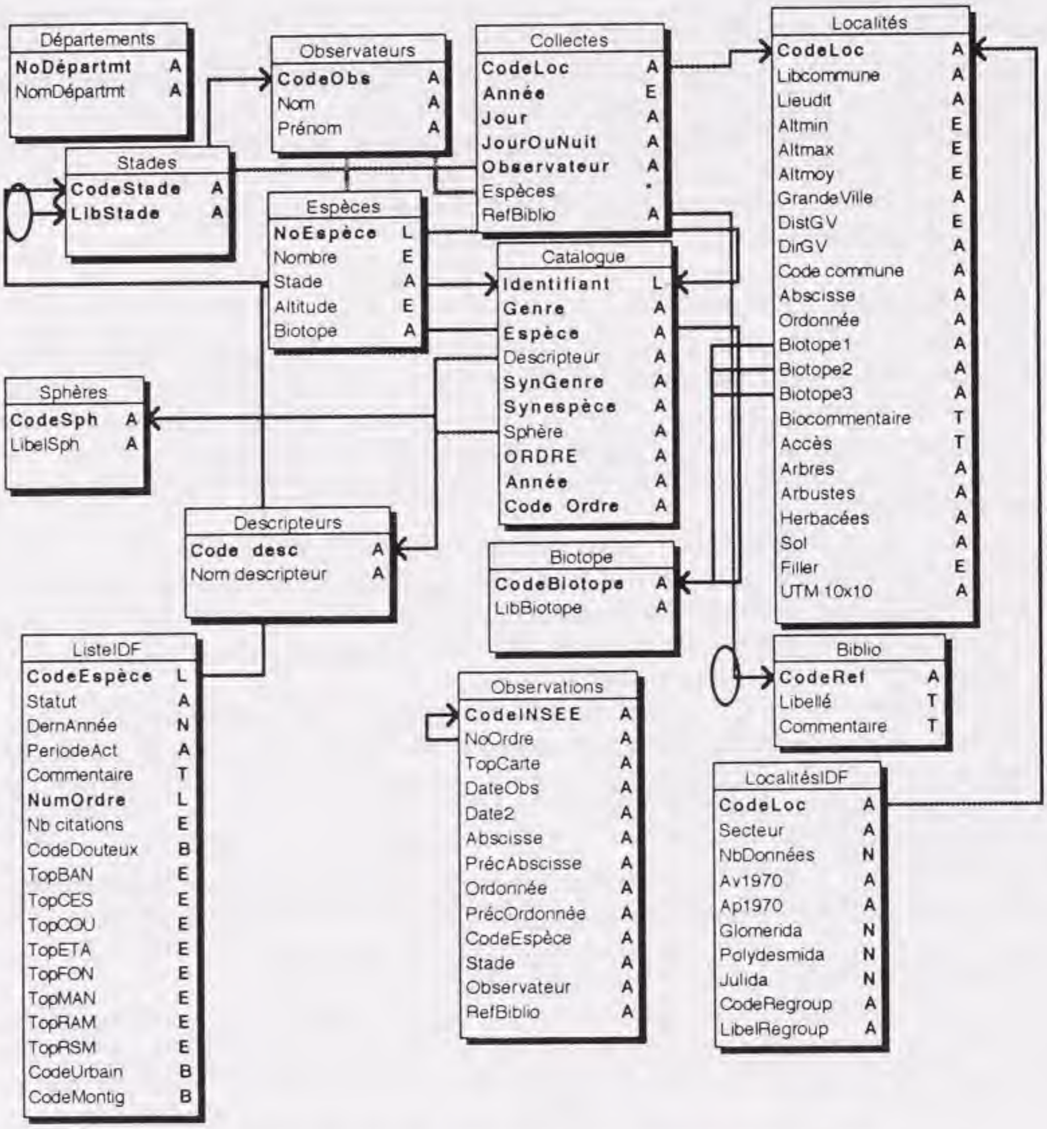


Fig. 1. — FAUNA GALLICA DIPLOPODA : main structure of the database.

— Biogeographical and ecogeographical spheres

According to a proposal from the European Council, France could be divided into 5 biogeographic areas: 1: Atlantic, 2: Continental, 3: Mediterranean, 4: Alpine & 5: Pyrenean. Despite the arbitrary nature of such a "biogeographic" division, it can facilitate the study of

Source : MNHN, Paris

addition, the relationships between species and environment are taken into account in 5 chosen large ecosystem types: 1: plains (s. l.), 2: coasts, 3: high mountains and high table-lands, 4: islands (Mediterranean, Atlantic and Channel Is.) & 5: caves (natural and artificial cave environments). As often shown and discussed before, subterranean ecosystems are one of the most important source of possible refuge for biodiversity (SERRA-COBO *et al.*, 1993), in natural caves or MSS compartments (GEOFFROY, 1984a, b; MAURIÈS & GEOFFROY, 1982) and artificial quarries as well (GEOFFROY, 1991).

CONCLUSION AND FUTURE PROSPECTS

The present work shows the preliminary steps towards a long-term comprehensive approach to the distribution and diversity of the millipede fauna of France. A large part of the data originate from reference collections (MNHN, Paris), bibliographic data-bases (CIM-Paris, BiblioMac-Milpat) and unpublished recent field collections. As the number of specialists is low for taxa such as Diplopoda and other myriapods groups, it seems important now to consider the possibility of establishing a more or less formal network of collectors in France. This would augment the data-bank, that could be centralized and studied by researchers in the MNHN laboratories at Paris and Brunoy.

Future developments can be summarised under four headings:

(i) Permanent updating of the check-list of millipede species, according to recent knowledge of millipede systematics and nomenclature.

(ii) Permanent updating of the "Provisional Departmental Atlas" of millipede species.

(iii) Progressive updating of the UTM grid cartography (10 km x 10 km).

(iv) Proposals for a precise zoogeographical distribution of species according to cartographic methods developed by the *Service du Patrimoine Naturel* (SPN: MNHN, Paris).

The FRENCH MILLIPEDE SURVEY and FAUNA GALLICA DIPLOPODA are tools for this purpose.

ANNEXE

Check-list of the French millipede species, from the data base FAUNA GALLICA DIPLOPODA (February 1996). In this list, *Geoglomeris subterranea* Verhoeff, 1908, is considered as a senior synonym of *Stygioglomeris crinita* Brölemann, 1913 and *Geoglomeris jurassica* Verhoeff, 1918.

1	*Lophoproctinus inferus*	Silvestri	1903	POLYXENIDA	Polyxenidea
2	*Lophoproctus jeanneli*	(Brölemann)	1910	POLYXENIDA	Polyxenidea
3	*Lophoproctus lucidus*	Chalande	1888	POLYXENIDA	Polyxenidea
4	*Polyxenus lagurus*	(Linné)	1758	POLYXENIDA	Polyxenidea
5	*Polyxenus macedonicus*	Verhoeff	1952	POLYXENIDA	Polyxenidea
6	*Adenomeris gibbosa*	Mauriès	1960	GLOMERIDA	Glomeridea
7	*Adenomeris hispida*	Ribaut	1909	GLOMERIDA	Glomeridea
8	*Corsikomeris remyi*	Verhoeff	1943	GLOMERIDA	Glomeridea
9	*Doderoa genuensis*	Silvestri	1904	GLOMERIDA	Glomeridea
10	*Geoglomeris duboscqui*	(Brölemann)	1913	GLOMERIDA	Glomeridea
11	*Geoglomeris granulosa*	(Ribaut)	1947	GLOMERIDA	Glomeridea
12	*Geoglomeris provincialis*	(Brölemann)	1913	GLOMERIDA	Glomeridea
13	*Geoglomeris subterranea*	Verhoeff	1908	GLOMERIDA	Glomeridea
14	*Glomeridella kervillei*	(Latzel)	1894	GLOMERIDA	Glomeridea
15	*Glomeris annulata*	Brandt	1833	GLOMERIDA	Glomeridea
16	*Glomeris connexa*	C.L.Koch	1847	GLOMERIDA	Glomeridea
17	*Glomeris conspersa*	C.L.Koch	1847	GLOMERIDA	Glomeridea
18	*Glomeris guttata*	Risso	1826	GLOMERIDA	Glomeridea
19	*Glomeris helvetica*	Verhoeff	1894	GLOMERIDA	Glomeridea
20	*Glomeris humbertiana*	Saussure	1893	GLOMERIDA	Glomeridea
21	*Glomeris intermedia*	Latzel	1884	GLOMERIDA	Glomeridea
22	*Glomeris marginata*	(Villers)	1789	GLOMERIDA	Glomeridea
23	*Glomeris pustulata*	Latreille	1804	GLOMERIDA	Glomeridea
24	*Glomeris transalpina*	C.L.Koch	1836	GLOMERIDA	Glomeridea
25	*Glomeris undulata*	C.L.Koch	1844	GLOMERIDA	Glomeridea
26	*Loboglomeris pyrenaica*	(Latzel)	1886	GLOMERIDA	Glomeridea
27	*Loboglomeris rugifera*	Verhoeff	1906	GLOMERIDA	Glomeridea
28	*Onychoglomeris castanea*	(Risso)	1826	GLOMERIDA	Glomeridea
29	*Protoglomeris vasconica*	(Brölemann)	1897	GLOMERIDA	Glomeridea

Source : MNHN, Paris

30	*Spelaeoglomeris alpina*	Brölemann	1913	GLOMERIDA	Glomeridea
31	*Spelaeoglomeris doderoi*	Silvestri	1908	GLOMERIDA	Glomeridea
32	*Spelaeoglomeris jeanneli*	Brölemann	1913	GLOMERIDA	Glomeridea
33	*Trachysphaera drescoi*	(Condé & Demange)	1961	GLOMERIDA	Glomeridea
34	*Trachysphaera lobata*	(Ribaut)	1954	GLOMERIDA	Glomeridea
35	*Trachysphaera pyrenaica*	(Ribaut)	1907	GLOMERIDA	Glomeridea
36	*Hirudisoma latum*	(Ribaut)	1908	POLYZONIIDA	Polyzoniidea
37	*Hirudisoma pyrenaeum*	(Ribaut)	1908	POLYZONIIDA	Polyzoniidea
38	*Polyzonium germanicum*	Brandt	1831	POLYZONIIDA	Polyzoniidea
39	*Fioria tuberculata*	Silvestri	1898	PLATYDESMIDA	Platydesmidea
40	*Callipus corsicus*	Verhoeff	1943	CALLIPODIDA	Callipodidea
41	*Callipus foetidissimus*	(Savi)	1819	CALLIPODIDA	Callipodidea
42	*Callipus sorrentinus*	Verhoeff	1910	CALLIPODIDA	Callipodidea
43	*Anamastigona pulchella*	Silvestri	1898	CHORDEUMATIDA	Craspedosomatidea
44	*Anthogona variegata*	Ribaut	1913	CHORDEUMATIDA	Craspedosomatidea
45	*Brachychaeteuma bagnalli*	Verhoeff	1911	CHORDEUMATIDA	Craspedosomatidea
46	*Brachychaeteuma bradae*	Brölemann & Brade-Birks	1917	CHORDEUMATIDA	Craspedosomatidea
47	*Brachychaeteuma cadurcensis*	Mauriès	1967	CHORDEUMATIDA	Craspedosomatidea
48	*Brachychaeteuma furcatum*	Ribaut	1956	CHORDEUMATIDA	Craspedosomatidea
49	*Brachychaeteuma melanops*	Brade-Birks & Brade-Birks	1918	CHORDEUMATIDA	Craspedosomatidea
50	*Brachychaeteuma peniculatum*	Ribaut	1949	CHORDEUMATIDA	Craspedosomatidea
51	*Brachychaeteuma plumosum*	Ribaut	1947	CHORDEUMATIDA	Craspedosomatidea
52	*Brachychaeteuma provinciale*	Ribaut	1956	CHORDEUMATIDA	Craspedosomatidea
53	*Broelemanneuma furcatum*	Ribaut	1913	CHORDEUMATIDA	Craspedosomatidea
54	*Broelemanneuma gayi*	Demange	1968	CHORDEUMATIDA	Craspedosomatidea
55	*Broelemanneuma gineti*	Ribaut	1954	CHORDEUMATIDA	Craspedosomatidea
56	*Broelemanneuma palmatum*	(Brölemann)	1902	CHORDEUMATIDA	Craspedosomatidea
57	*Broelemanneuma pectiniger*	(Brölemann)	1902	CHORDEUMATIDA	Craspedosomatidea
58	*Camptogona delamarei*	Mauriès	1969	CHORDEUMATIDA	Craspedosomatidea
59	*Camptogona duboscqui*	(Brölemann)	1903	CHORDEUMATIDA	Craspedosomatidea
60	*Ceratosphys amoena*	Ribaut	1920	CHORDEUMATIDA	Craspedosomatidea
61	*Ceratosphys banyulsensis*	Brolemann	1926	CHORDEUMATIDA	Craspedosomatidea
62	*Ceratosphys guttata*	Ribaut	1956	CHORDEUMATIDA	Craspedosomatidea
63	*Ceratosphys nivium*	Ribaut	1927	CHORDEUMATIDA	Craspedosomatidea
64	*Ceratosphys picta*	Ribaut	1951	CHORDEUMATIDA	Craspedosomatidea
65	*Ceratosphys simoni*	Ribaut	1920	CHORDEUMATIDA	Craspedosomatidea
66	*Ceratosphys vandeli*	Mauriès	1963	CHORDEUMATIDA	Craspedosomatidea
67	*Chamaesoma broelemanni*	Ribaut & Verhoeff	1913	CHORDEUMATIDA	Craspedosomatidea
68	*Corsicosoma legeri*	(Brölemann)	1903	CHORDEUMATIDA	Craspedosomatidea
69	*Cranogona dalensi*	Mauriès	1965	CHORDEUMATIDA	Craspedosomatidea
70	*Cranogona delicata*	Mauriès	1963	CHORDEUMATIDA	Craspedosomatidea
71	*Cranogona denticulata*	Delmas	1925	CHORDEUMATIDA	Craspedosomatidea
72	*Cranogona orientale*	Ribaut	1913	CHORDEUMATIDA	Craspedosomatidea
73	*Cranogona pavida*	Ribaut	1951	CHORDEUMATIDA	Craspedosomatidea
74	*Cranogona touyaensis*	Mauriès	1975	CHORDEUMATIDA	Craspedosomatidea
75	*Cranogona uncinata*	Ribaut	1951	CHORDEUMATIDA	Craspedosomatidea
76	*Cranogona vasconica*	Ribaut	1913	CHORDEUMATIDA	Craspedosomatidea
77	*Craspedosoma alemannicum*	Verhoeff	1910	CHORDEUMATIDA	Craspedosomatidea
78	*Craspedosoma rawlinsii*	Leach	1814	CHORDEUMATIDA	Craspedosomatidea
79	*Craspedosoma taurinorum conforme*	Silvestri	1898	CHORDEUMATIDA	Craspedosomatidea
80	*Crossosoma broelemanni*	Strasser	1975	CHORDEUMATIDA	Craspedosomatidea
81	*Crossosoma cavernicola*	Manfredi	1951	CHORDEUMATIDA	Craspedosomatidea
82	*Crossosoma mauriesi*	Strasser	1970	CHORDEUMATIDA	Craspedosomatidea
83	*Crossosoma peyerimhoffi*	(Brölemann)	1902	CHORDEUMATIDA	Craspedosomatidea
84	*Cyrnosoma beroni*	Mauriès	1969	CHORDEUMATIDA	Craspedosomatidea
85	*Cyrnosoma coineaui*	Mauriès	1969	CHORDEUMATIDA	Craspedosomatidea
86	*Cyrnosoma strasseri*	Mauriès	1969	CHORDEUMATIDA	Craspedosomatidea
87	*Escualdosoma gourbaultae*	Mauriès	1965	CHORDEUMATIDA	Craspedosomatidea
88	*Haasea flavescens*	(Latzel)	1882	CHORDEUMATIDA	Craspedosomatidea
89	*Helvetiosoma arvernum*	(Ribaut & Brolemann)	1932	CHORDEUMATIDA	Craspedosomatidea
90	*Hispaniosoma racovitzai*	Ribaut	1913	CHORDEUMATIDA	Craspedosomatidea
91	*Hypnosoma exornatum*	Ribaut	1952	CHORDEUMATIDA	Craspedosomatidea
92	*Hypnosoma juberthieorum*	Mauriès	1968	CHORDEUMATIDA	Craspedosomatidea
93	*Hypnosoma pallidum*	Ribaut	1952	CHORDEUMATIDA	Craspedosomatidea
94	*Iulogona tirolensis cisalpinum*	(Brolemann)	1930	CHORDEUMATIDA	Craspedosomatidea
95	*Janetschekella valesiaca*	(Faës)	1902	CHORDEUMATIDA	Craspedosomatidea
96	*Marquetiella auriculata*	(Ribaut)	1920	CHORDEUMATIDA	Craspedosomatidea
97	*Marquetiella lunata*	(Ribaut)	1920	CHORDEUMATIDA	Craspedosomatidea
98	*Marquetiella pyrenaica*	(Ribaut)	1905	CHORDEUMATIDA	Craspedosomatidea
99	*Nanogona balazuci*	(Schubart)	1958	CHORDEUMATIDA	Craspedosomatidea
100	*Nanogona cebennica*	(Ribaut)	1947	CHORDEUMATIDA	Craspedosomatidea
101	*Nanogona davidi*	(Demange)	1967	CHORDEUMATIDA	Craspedosomatidea
102	*Nanogona digitata*	(Ribaut)	1913	CHORDEUMATIDA	Craspedosomatidea
103	*Nanogona polydesmoides*	(Leach)	1814	CHORDEUMATIDA	Craspedosomatidea
104	*Nanogona uncinata*	(Ribaut)	1913	CHORDEUMATIDA	Craspedosomatidea
105	*Ochogona gallitarum*	(Brölemann)	1900	CHORDEUMATIDA	Craspedosomatidea
106	*Opisthocheiron canayerensis*	Mauriès & Geoffroy	1982	CHORDEUMATIDA	Craspedosomatidea
107	*Opisthocheiron cornutum*	Ribaut	1922	CHORDEUMATIDA	Craspedosomatidea
108	*Opisthocheiron elegans*	Ribaut	1922	CHORDEUMATIDA	Craspedosomatidea
109	*Opisthocheiron fallax*	Ribaut	1922	CHORDEUMATIDA	Craspedosomatidea
110	*Opisthocheiron lacazei*	Brolemann	1932	CHORDEUMATIDA	Craspedosomatidea
111	*Opisthocheiron penicillatum*	Ribaut	1913	CHORDEUMATIDA	Craspedosomatidea
112	*Origmatogona kimeorum*	Mauriès	1990	CHORDEUMATIDA	Craspedosomatidea
113	*Pyreneosoma barbieri*	Mauriès	1970	CHORDEUMATIDA	Craspedosomatidea
114	*Pyreneosoma bessoni*	Mauriès	1974	CHORDEUMATIDA	Craspedosomatidea
115	*Pyreneosoma digitatum*	Mauriès	1959	CHORDEUMATIDA	Craspedosomatidea
116	*Pyreneosoma ribauti*	Mauriès	1959	CHORDEUMATIDA	Craspedosomatidea

Source : MNHN, Paris

117	*Pyrgocyphosoma dalmazzense*	Verhoeff	1930	CHORDEUMATIDA	Craspedosomatidea
118	*Pyrgocyphosoma doriae*	(Silvestri)	1898	CHORDEUMATIDA	Craspedosomatidea
119	*Rhymogona cervina*	(Verhoeff)	1910	CHORDEUMATIDA	Craspedosomatidea
120	*Rhymogona alemannica*	(Verhoeff)	1910	CHORDEUMATIDA	Craspedosomatidea
121	*Rhymogona montivaga*	(Verhoeff)	1894	CHORDEUMATIDA	Craspedosomatidea
122	*Scutogona jeanneli*	Ribaut	1913	CHORDEUMATIDA	Craspedosomatidea
123	*Semiosoma bardei*	Ribaut	1913	CHORDEUMATIDA	Craspedosomatidea
124	*Semiosoma devillei*	(Brölemann)	1901	CHORDEUMATIDA	Craspedosomatidea
125	*Vandeleuma vasconicum*	Mauriès	1966	CHORDEUMATIDA	Craspedosomatidea
126	*Vascosoma coiffaiti*	Mauriès	1966	CHORDEUMATIDA	Craspedosomatidea
127	*Vascosoma coiffaiti falsaforma*	Mauriès	1990	CHORDEUMATIDA	Craspedosomatidea
128	*Vascosoma duprei*	Mauriès	1990	CHORDEUMATIDA	Craspedosomatidea
129	*Xylophageuma zschokkei*	Bigler	1912	CHORDEUMATIDA	Craspedosomatidea
130	*Xystrosoma beatense*	Ribaut	1927	CHORDEUMATIDA	Craspedosomatidea
131	*Xystrosoma cassagnaui*	Mauriès	1965	CHORDEUMATIDA	Craspedosomatidea
132	*Xystrosoma catalonicum*	Ribaut	1927	CHORDEUMATIDA	Craspedosomatidea
133	*Xystrosoma muricum*	Ribaut	1927	CHORDEUMATIDA	Craspedosomatidea
134	*Xystrosoma pyrenaicum*	Ribaut	1927	CHORDEUMATIDA	Craspedosomatidea
135	*Xystrosoma tectosagum*	Ribaut	1927	CHORDEUMATIDA	Craspedosomatidea
136	*Chordeuma consoranense*	Ribaut	1956	CHORDEUMATIDA	Chordeumatidea
137	*Chordeuma iluronense*	Ribaut	1913	CHORDEUMATIDA	Chordeumatidea
138	*Chordeuma inornatum*	Ribaut	1913	CHORDEUMATIDA	Chordeumatidea
139	*Chordeuma intermedium*	Ribaut	1913	CHORDEUMATIDA	Chordeumatidea
140	*Chordeuma montanum*	Ribaut	1956	CHORDEUMATIDA	Chordeumatidea
141	*Chordeuma muticum*	Ribaut	1913	CHORDEUMATIDA	Chordeumatidea
142	*Chordeuma proximum*	Ribaut	1913	CHORDEUMATIDA	Chordeumatidea
143	*Chordeuma reflexum*	Brolemann	1927	CHORDEUMATIDA	Chordeumatidea
144	*Chordeuma silvestre*	C. Koch	1847	CHORDEUMATIDA	Chordeumatidea
145	*Chordeuma trifidum*	Ribaut	1913	CHORDEUMATIDA	Chordeumatidea
146	*Chordeuma utriculosum*	Ribaut	1913	CHORDEUMATIDA	Chordeumatidea
147	*Chordeuma vasconicum*	Ribaut	1913	CHORDEUMATIDA	Chordeumatidea
148	*Melogona gallica*	(Latzel)	1884	CHORDEUMATIDA	Chordeumatidea
149	*Melogona scutellare*	(Ribaut)	1913	CHORDEUMATIDA	Chordeumatidea
150	*Mycogona germanica*	(Verhoeff)	1892	CHORDEUMATIDA	Chordeumatidea
151	*Orthochordeumella fulva*	(Rothenbühler)	1899	CHORDEUMATIDA	Chordeumatidea
152	*Orthochordeumella leclerci*	Mauriès	1979	CHORDEUMATIDA	Chordeumatidea
153	*Orthochordeumella pallida*	(Rothenbühler)	1899	CHORDEUMATIDA	Chordeumatidea
154	*Orthochordeumella pyrenaica*	Mauriès	1965	CHORDEUMATIDA	Chordeumatidea
155	*Parachordeuma broelemanni*	Ribaut	1912	CHORDEUMATIDA	Chordeumatidea
156	*Oxidus gracilis*	(C.L. Koch)	1847	POLYDESMIDA	Paradoxosomatidea
157	*Stosatea italica*	(Latzel)	1886	POLYDESMIDA	Paradoxosomatidea
158	*Archipolydesmus ribauti*	(Brolemann)	1926	POLYDESMIDA	Polydesmidea
159	*Brachydesmus exiguus*	Brölemann	1894	POLYDESMIDA	Polydesmidea
160	*Brachydesmus proximus*	Latzel	1889	POLYDESMIDA	Polydesmidea
161	*Brachydesmus superus*	Latzel	1884	POLYDESMIDA	Polydesmidea
162	*Devillea tuberculata*	Brölemann	1902	POLYDESMIDA	Polydesmidea
163	*Eumastigonodesmus boncii*	(Brölemann)	1908	POLYDESMIDA	Polydesmidea
164	*Galliocookia balazuci*	Mauriès	1983	POLYDESMIDA	Polydesmidea
165	*Galliocookia fagei*	Ribaut	1954	POLYDESMIDA	Polydesmidea
166	*Galliocookia leclerci*	Mauriès	1983	POLYDESMIDA	Polydesmidea
167	*Macrosternodesmus palicola*	Brölemann	1908	POLYDESMIDA	Polydesmidea
168	*Mastigonodesmus destefani*	Silvestri	1898	POLYDESMIDA	Polydesmidea
169	*Mastigonodesmus fagniezi*	Mauriès	1982	POLYDESMIDA	Polydesmidea
170	*Mastigonodesmus lopezi*	Mauriès	1980	POLYDESMIDA	Polydesmidea
171	*Occitanocookia hirsuta*	(Ribaut)	1948	POLYDESMIDA	Polydesmidea
172	*Ophiodesmus albonanus*	(Latzel)	1895	POLYDESMIDA	Polydesmidea
173	*Perapolydesmus progressus*	(Brölemann)	1900	POLYDESMIDA	Polydesmidea
174	*Polydesmus angustus*	Latzel	1884	POLYDESMIDA	Polydesmidea
175	*Polydesmus asthenestatus*	Pocock	1894	POLYDESMIDA	Polydesmidea
176	*Polydesmus barbierii*	Latzel	1889	POLYDESMIDA	Polydesmidea
177	*Polydesmus coriaceus*	Porath	1870	POLYDESMIDA	Polydesmidea
178	*Polydesmus corsicus*	Schubart	1931	POLYDESMIDA	Polydesmidea
179	*Polydesmus denticulatus*	C. Koch	1847	POLYDESMIDA	Polydesmidea
180	*Polydesmus germanicus*	Verhoeff	1896	POLYDESMIDA	Polydesmidea
181	*Polydesmus helveticus*	Verhoeff	1894	POLYDESMIDA	Polydesmidea
182	*Polydesmus incisus*	Brolemann	1921	POLYDESMIDA	Polydesmidea
183	*Polydesmus inconstans*	Latzel	1884	POLYDESMIDA	Polydesmidea
184	*Polydesmus mistrei*	Brölemann	1902	POLYDESMIDA	Polydesmidea
185	*Polydesmus niveus*	Brölemann	1900	POLYDESMIDA	Polydesmidea
186	*Polydesmus plicatus*	Ceuca	1962	POLYDESMIDA	Polydesmidea
187	*Polydesmus racovitzai*	Brölemann	1910	POLYDESMIDA	Polydesmidea
188	*Polydesmus raffardi*	Brölemann	1905	POLYDESMIDA	Polydesmidea
189	*Polydesmus taranus*	Verhoeff	1936	POLYDESMIDA	Polydesmidea
190	*Polydesmus testaceus*	C.L.Koch	1847	POLYDESMIDA	Polydesmidea
191	*Polydesmus troglobius*	Latzel	1889	POLYDESMIDA	Polydesmidea
192	*Alpiobates peyerimhoffi*	(Brölemann)	1900	JULIDA	Blaniulidea
193	*Archiboreoiulus pallidus*	(Brade-Birks)	1920	JULIDA	Blaniulidea
194	*Archiboreoiulus sollaudi*	Brolemann	1921	JULIDA	Blaniulidea
195	*Boreoiulus dollfusi*	Brölemann	1895	JULIDA	Blaniulidea
196	*Blaniulus guttulatus*	(Fabricius)	1798	JULIDA	Blaniulidea
197	*Blaniulus lichtensteini*	Brolemann	1921	JULIDA	Blaniulidea
198	*Blaniulus lorifer*	Brolemann	1921	JULIDA	Blaniulidea
199	*Blaniulus mayeti*	(Brölemann)	1902	JULIDA	Blaniulidea
200	*Blaniulus orientalis*	Brölemann	1921	JULIDA	Blaniulidea
201	*Blaniulus troglobius*	(Latzel)	1886	JULIDA	Blaniulidea
202	*Blaniulus troglodites*	Brölemann	1898	JULIDA	Blaniulidea
203	*Blaniulus velatus*	Ribaut	1954	JULIDA	Blaniulidea

Source : MNHN, Paris

204	*Blaniulus virei*	Brölemann	1900	JULIDA	Blaniulidea
205	*Boreoiulus simplex*	Brolemann	1921	JULIDA	Blaniulidea
206	*Boreoiulus tenuis*	(Bigler)	1913	JULIDA	Blaniulidea
207	*Choneiulus palmatus*	(Nemec)	1895	JULIDA	Blaniulidea
208	*Choneiulus subterraneus*	(Silvestri)	1903	JULIDA	Blaniulidea
209	*Galliobates gracilis*	Ribaut	1909	JULIDA	Blaniulidea
210	*Iberoiulus sarensis*	Mauriès	1970	JULIDA	Blaniulidea
211	*Mesoblaniulus serrula*	(Brölemann)	1905	JULIDA	Blaniulidea
212	*Monacobates monoecensis*	(Brölemann)	1905	JULIDA	Blaniulidea
213	*Thalassisobates littoralis*	(Silvestri)	1903	JULIDA	Blaniulidea
214	*Nemasoma varicorne*	C.L.Koch	1847	JULIDA	Blaniulidea
215	*Nopoiulus kochii*	(Gervais)	1847	JULIDA	Blaniulidea
216	*Occitaniulus rouchi*	Brolemann	1923	JULIDA	Blaniulidea
217	*Proteroiulus broelemanni*	Lohmander	1925	JULIDA	Blaniulidea
218	*Proteroiulus fuscus*	(Am Stein)	1857	JULIDA	Blaniulidea
219	*Trichoblaniulus hirsutus*	(Brölemann)	1889	JULIDA	Blaniulidea
220	*Trichoblaniulus lanuginosus*	Ribaut	1947	JULIDA	Blaniulidea
221	*Vascoblaniulus cabidochei*	Mauriès	1967	JULIDA	Blaniulidea
222	*Allajulus nitidus*	(Verhoeff)	1891	JULIDA	Julidea
223	*Brachyiulus lusitanus*	(Verhoeff)	1898	JULIDA	Julidea
224	*Brachyiulus pusillus*	(Leach)	1815	JULIDA	Julidea
225	*Cylindroiulus broti*	(Humbert)	1893	JULIDA	Julidea
226	*Cylindroiulus caeruleocinctus*	(Wood)	1864	JULIDA	Julidea
227	*Cylindroiulus chalandei*	(Ribaut)	1904	JULIDA	Julidea
228	*Cylindroiulus iluronensis*	Brölemann	1912	JULIDA	Julidea
229	*Cylindroiulus latestriatus*	(Curtis)	1844	JULIDA	Julidea
230	*Cylindroiulus limitaneus*	(Brölemann)	1905	JULIDA	Julidea
231	*Cylindroiulus londinensis*	(Leach)	1814	JULIDA	Julidea
232	*Cylindroiulus parisiorum*	(Brölemann & Verhoeff)	1896	JULIDA	Julidea
233	*Cylindroiulus punctatus*	(Leach)	1815	JULIDA	Julidea
234	*Cylindroiulus pyrenaicus*	Brölemann	1897	JULIDA	Julidea
235	*Cylindroiulus sagittarius*	Brölemann	1897	JULIDA	Julidea
236	*Cylindroiulus schubarti*	Verhoeff	1943	JULIDA	Julidea
237	*Cylindroiulus segregatus*	Brölemann	1903	JULIDA	Julidea
238	*Cylindroiulus spinosus*	(Ribaut)	1904	JULIDA	Julidea
239	*Cylindroiulus verhoeffi*	(Brölemann)	1896	JULIDA	Julidea
240	*Cylindroiulus vulnerarius*	(Berlese)	1888	JULIDA	Julidea
241	*Dolichoiulus tongiorgii*	(Strasser)	1973	JULIDA	Julidea
242	*Enantiulus armatus*	(Ribaut)	1909	JULIDA	Julidea
243	*Enantiulus nanus*	(Latzel)	1884	JULIDA	Julidea
244	*Haplopodoiulus spathifer*	(Brölemann)	1897	JULIDA	Julidea
245	*Hypsoiulus alpivagus*	(Verhoeff)	1897	JULIDA	Julidea
246	*Julus scandinavius*	Latzel	1884	JULIDA	Julidea
247	*Leptoiulus arelatus*	Bigler	1919	JULIDA	Julidea
248	*Leptoiulus belgicus*	(Latzel)	1884	JULIDA	Julidea
249	*Leptoiulus bertkaui*	(Verhoeff)	1896	JULIDA	Julidea
250	*Leptoiulus brevivelatus*	Bigler	1919	JULIDA	Julidea
251	*Leptoiulus bruyanti*	Ribaut	1951	JULIDA	Julidea
252	*Leptoiulus demangei*	Schubart	1962	JULIDA	Julidea
253	*Leptoiulus garumnicus*	(Ribaut)	1904	JULIDA	Julidea
254	*Leptoiulus juvenilis*	(Ribaut)	1908	JULIDA	Julidea
255	*Leptoiulus kervillei*	(Brölemann)	1896	JULIDA	Julidea
256	*Leptoiulus legeri*	(Brölemann)	1897	JULIDA	Julidea
257	*Leptoiulus meridionalis*	(Brölemann)	1897	JULIDA	Julidea
258	*Leptoiulus montivagus*	(Latzel)	1884	JULIDA	Julidea
259	*Leptoiulus odieri*	(Brölemann)	1896	JULIDA	Julidea
260	*Leptoiulus piceus*	(Risso)	1826	JULIDA	Julidea
261	*Leptoiulus remyi*	Schubart	1962	JULIDA	Julidea
262	*Leptoiulus simplex glacialis*	(Verhoeff)	1894	JULIDA	Julidea
263	*Leptoiulus umbratilis*	(Ribaut)	1905	JULIDA	Julidea
264	*Leptoiulus uncinatus*	Ribaut	1951	JULIDA	Julidea
265	*Metaiulus pratensis*	Blower & Rolfe	1956	JULIDA	Julidea
266	*Ommatoiulus albolineatus*	(Lucas)	1845	JULIDA	Julidea
267	*Ommatoiulus corsicus*	(Brölemann)	1903	JULIDA	Julidea
268	*Ommatoiulus hauckeri*	Mauriès	1969	JULIDA	Julidea
269	*Ommatoiulus illicis*	(Brölemann)	1897	JULIDA	Julidea
270	*Ommatoiulus imminutus*	(Brolemann)	1926	JULIDA	Julidea
271	*Ommatoiulus lienhardti*	(Brolemann)	1921	JULIDA	Julidea
272	*Ommatoiulus rutilans*	(C.L.Koch)	1847	JULIDA	Julidea
273	*Ommatoiulus sabulosus*	(Linné)	1758	JULIDA	Julidea
274	*Ophyiulus bastiensis*	Verhoeff	1943	JULIDA	Julidea
275	*Ophyiulus chilopogon*	(Latzel)	1884	JULIDA	Julidea
276	*Ophyiulus corsicus*	Verhoeff	1943	JULIDA	Julidea
277	*Ophyiulus napolitanus*	(Attems)	1903	JULIDA	Julidea
278	*Ophyiulus pilosus*	(Newport)	1842	JULIDA	Julidea
279	*Ophyiulus renosensis*	Mauriès	1969	JULIDA	Julidea
280	*Pachyiulus varius*	(Fabricius)	1781	JULIDA	Julidea
281	*Tachypodoiulus niger*	(Leach)	1815	JULIDA	Julidea
282	*Typhloiulus sculterorum*	(Brölemann)	1905	JULIDA	Julidea

Source : MNHN, Paris

ACKNOWLEGEMENTS

I am very grateful to my colleagues J. P. MAURIÈS (Paris), R. D. KIME (Bruxelles) and A. PEDROLI-CHRISTEN (Neuchâtel) for providing new localities and information. Many thanks to P. MOTHIRON for discussions and advice related to the computer database. Comments of Prof. J. G. BLOWER and Dr. A. D. BARBER on the English version of this manuscript are gratefully acknowledged.

REFERENCES

BARBAULT, R., 1994. — *Des baleines, des bactéries et des hommes*. Paris, Odile Jacob, Sciences, 327 pp.

BLANDIN, P., 1989. — Sur la richesse spécifique et la rareté comme critères d'évaluation de systèmes écologiques. *In* : F. DE BEAUFORT & H. MAURIN, *Utilisation des inventaires d'invertébrés pour l'identification et la surveillance d'espaces de grand intérêt faunistique*. Paris, SFF, MNHN : 71-80.

BLOWER, J. G., 1985. — *Millipedes* (*Synopses of the Br. Fauna* NS, **35**). London, E. J. Brill & W. Backhuys, 242 pp.

BRITISH MYRIAPOD GROUP, 1988. — *Preliminary Atlas of the Millipedes of the British Isles*. Huntingdon, NERC, 65 pp.

CULVER, D. C. & HOLSINGER, J. R., 1992. — How many species of troglobites are there? *NSS Bulletin*, **54** : 79-80.

ENGHOFF, H., 1974. — Om tusindbenenes udbredelse i Danmark (Diplopoda). *Ent. Meddr.*, **42** : 21-32.

ERWIN, T. L., 1988. — The tropical forest canopy: the heart of biotic diversity. *In* : E. O. WILSON, *Biodiversity*. Washington D. C., National Academic Press : 123-129.

GEOFFROY, J. J., 1981. — Les myriapodes du Parc national des Ecrins. I. Stations de récolte (1976-1979) et présentation générale des peuplements de chilopodes et de diplopodes. *Trav. Sci. Parc Natl. Ecrins*, **1** : 97-123.

GEOFFROY, J. J., 1984a. — Particularités du développement post-embryonnaire du diplopode craspédosomide cavernicole *Opisthocheiron canayerensis*. *Mém. Biospéol.*, **11** : 211-220.

GEOFFROY, J. J., 1984b. — *Opisthocheiron canayerensis* (Diplopoda : Craspedosomatida) : répartition de l'espèce et variations de la pigmentation. *Mém. Biospéol.*, **11** : 295-302.

GEOFFROY, J. J.,1989. — La faune des diplopodes de France. 2 : projet de cartographie des espèces. *In* : F. DE BEAUFORT & H. MAURIN, *Utilisation des inventaires d'invertébrés pour l'identification et la surveillance d'espaces de grand intérêt faunistique*. Paris, SFF, MNHN : 270-271.

GEOFFROY, J. J., 1990a. — La faune des diplopodes de France : un bilan des espèces. *In* : A. MINELLI, *Proc. 7th Int. Congr. Myriapodology*. Leiden, Brill : 345-359.

GEOFFROY, J. J., 1990b. — Les diplopodes cavernicoles de France. *Mém. Biospéol.*, **17** : 3-11.

GEOFFROY, J. J., 1991. — Les cavités artificielles et la répartition des diplopodes endogés et souterrains : intérêt biogéographique. *Rev. Suisse Zool.*, **98** : 93-106.

GEOFFROY, J. J., 1992. — Clé d'identification des classes de myriapodes et des ordres de chilopodes fréquents dans le sol et ses annexes. *Millepattia*, **1** : 23-37.

GEOFFROY, J. J., 1993a. — Clés d'identification des ordres de diplopodes fréquents dans le sol. (Myriapoda ; Diplopoda). *Millepattia*, **2** : 4-28.

GEOFFROY, J. J., 1993b. — L'inventaire et la cartographie des diplopodes de France. *In*: : J. LHONORÉ, H. MAURIN, R GUILBOT & P. KEITH, *Inventaire et cartographie des invertébrés comme contribution à la gestion des milieux naturels français. Coll. Patrimoines Naturels*, **13**. Paris, SSF / MNHN : 144-148.

GEOFFROY, J. J., 1994a. — Steps towards a comprehensive distribution of soil and cave-dwelling Diplopoda species. A perspective on millipede biodiversity in France. *In* : G. MESSANA & S. TAITI, *XI International Symposium of Biospeology, Firenze, Castello di Montegufoni, 28 August - 2 September 1994 (Italy), Abstracts* Firenze, Università degli Studi di Firenze (65pp.).

GEOFFROY, J. J., 1994b. — FAUNA GALLICA DIPLOPODA : Étapes pour une étude de la répartition et de la biodiversité des diplopodes de France. *In* : B. CONDÉ, *98ème Journées de la Société Zoologique de France, Nancy, 4-5-6 Juillet 1994, Résumé des communications* Nancy, Université Henri Poincaré : 55.

GEOFFROY, J. J., & MAURIÈS, J. P., 1992. — Les diplopodes édaphiques et souterrains de France : données récentes, répartition des espèces nouvellement décrites et peu connues. *Mém. Biospéol.*, **19** : 127-133.

GONSETH, Y., 1993. — Le CSCF, un relai entre les recherches éco-faunistiques et la pratique. *In*: : J. LHONORÉ, H. MAURIN, R. GUILBOT & P. KEITH, *Inventaire et cartographie des invertébrés comme contribution à la gestion des milieux naturels français. Coll. Patrimoines Naturels*, **13**. Paris, SSF / MNHN : 51-57.

JEEKEL, C. A. W., 1978. — Voorlopige atlas van de verspreiding der Nederlandse miljoenpoten (Diplopoda). *Verslagen en Technische Gegevens*, **15**. Amsterdam, Instituut voor Taxonomische Zoölogie, 68 pp.

JUBERTHIE, C. & DECU, V., 1994. — Structure et diversité du domaine souterrain ; particularités des habitats et adaptations des espèces. *In* : C. JUBERTHIE & V. DECU, *Encyclopædia Biospeologica, Tome 1*. Moulis-Bucarest, Société de Biospéologie : 5-22.

Source : MNHN, Paris

KIME, R. D., 1990. — *A provisional atlas of European myriapods, Part 1.* Luxembourg, European Invertebrate Survey, 109pp.

LÉVÊQUE, C., 1994. — *Environnement et diversité du vivant.* Paris, CSI Pocket / ORSTOM, 127 pp.

MAURER, B. A., 1994. — *Geographical population analysis: tools for the analysis of biodiversity.* Oxford, Blackwell Scientific Publications, 130pp.

MAURIÈS, J. P., 1982. — *Dolichoiulus tongiorgii* (Strasser), diplopode halophile nouveau pour la faune de France. Remarques sur la classification des Pachyiulini. *Bull. Mus. natl. Hist. nat., Paris, (A)*, **4** : 433-444.

MAURIÈS, J. P. & GEOFFROY, J. J., 1982. — Découverte, dans les Causses Majeurs, d'une remarquable espèce cavernicole du genre *Opisthocheiron* Ribaut, 1913 (Diplopoda, Craspedosomida, Opisthocheiridae). *Bull. Soc. Hist. nat. Toulouse*, **118** : 131-140.

MAURIN, H. & GUILBOT, R., 1993. — La cartographie des invertébrés et la gestion des milieux naturels. *In*: : J. LHONORÉ, H. MAURIN, R. GUILBOT & P. KEITH, *Inventaire et cartographie des invertébrés comme contribution à la gestion des milieux naturels français. Coll. Patrimoines Naturels,* **13**. Paris, SSF / MNHN : 9-17.

MAY, R. M., 1992. — L'inventaire des espèces vivantes. *Pour la Science*, **182** : 30-36.

MOTHIRON, P., 1993. — Un exemple régional : l'inventaire des lépidoptères d'Île-de-France. *In*: : J. LHONORÉ, H. MAURIN, R. GUILBOT & P. KEITH, *Inventaire et cartographie des invertébrés comme contribution à la gestion des milieux naturels français. Coll. Patrimoines Naturels,* **13**. Paris, SSF / MNHN : 103-105.

PEDROLI-CHRISTEN, A., 1993. — *Faunistique des mille-pattes de Suisse (Diplopoda) / Faunistik der Tausendfüssler der Schweiz (Diplopoda).* Neuchâtel, Centre Suisse de Cartographie de la Faune, *Doc. faun. helv.*, **14**, 248 pp.

RASMONT, P., 1993. — Méthodologie et outillage de la cartographie écologique des invertébrés. *In*: : J. LHONORÉ, H. MAURIN, R. GUILBOT & P. KEITH, *Inventaire et cartographie des invertébrés comme contribution à la gestion des milieux naturels français. Coll. Patrimoines Naturels,* **13**. Paris, SSF / MNHN : 28-50.

REMY, P. & HOFFMAN, J., 1959. — Faune des Myriapodes du Grand-Duché de Luxembourg. *Archives de la Section des Sciences de l'Institut Grand-Ducal*, **26** : 199-236.

SERRA-COBO, J., BARBAULT, R. & ESTRADA-PENA, A., 1993. — Le gouffre de San Pedro de Los Griegos (Oliete, Teruel, Espagne) : un refuge de biodiversité sans équivalent en Europe. *Rev. Ecol. (Terre Vie)*, **48** : 341-348.

SCHUBART, O., 1934. — Tausendfüssler oder Myriapoda. I: Diplopoda. *Tierwelt Deutchl.*, **28** : i-viii + 1-318.

SOLBRIG, O. T., van EMDEN, H. M. & van OORDT, P. G., (eds), 1992. — *Biodiversity and Global Change.* Paris, *IUBS Monographs*, **8**.

STRASSER, C. & MINELLI, A., 1984. — Elenco dei diplopodi d'Italia. *Lavori-Soc. Ven. Sc. nat.*, **9** : 193-212.

WILSON, E. O, 1993. — *La diversité de la vie.* Paris, Odile Jacob, Sciences, 496 pp.

Source : MNHN, Paris

Faunistique des mille-pattes de Suisse (Diplopoda) - Faunistik der Tausendfüssler der Schweiz (Diplopoda)

Ariane PEDROLI-CHRISTEN

C.S.C.F., Musée d'Histoire Naturelle, Terreaux 14, CH-2000 Neuchâtel, Switzerland

RÉSUMÉ

Une synthèse et un constat actuel et critique des connaissances relatives aux diplopodes de Suisse sont proposés dans cet ouvrage (PEDROLI-CHRISTEN, 1993), tant du point de vue systématique, chorologique qu'écologique. Si l'origine des données permettant cette évaluation est très disparate (données bibliographiques, collections, récoltes récentes), l'ampleur des observations permet cependant d'effectuer une analyse quantitative. Le catalogue complet des 14300 données est déposé au Centre Suisse de Cartographie de la Faune, CSCF. La composition de la faune des diplopodes de Suisse peut être considérée actuellement comme relativement bien connue : 127 taxons identifiés sont répartis dans 6 ordres et 18 familles. Plusieurs difficultés systématiques ont été mises en évidence, dues au concept purement typologique de l'espèce, généralement en vigueur en myriapodologie. Elles sont également l'expression de l'importance des facteurs historiques sur ce groupe. Pour chaque espèce, les résultats obtenus sont discutés et illustrés selon un schéma standard : rapide synonymie, références bibliographiques synthétiques des meilleures descriptions et illustrations, références bibliographiques helvétiques, aspects chorologiques, écologiques et phénologiques, tableau synthétique du nombre d'observations effectives et carte de répartition. Une étude qualitative de l'ensemble de la faune reprend plusieurs des paramètres retenus dans l'analyse par espèce en considérant cette fois l'organisation des peuplements. Divers groupements d'espèces sont ainsi proposés selon leur répartition géographique, leur distribution altitudinale et les types de milieux colonisés.

ABSTRACT

Faunistics of the Swiss millipedes (Diplopoda).

An up-to-date and critical synthesis of the present knowledge of the Swiss Diplopoda is given in this book (PEDROLI-CHRISTEN, 1993) in the scope systematics, distribution and ecology. In spite of the lack of uniformity of the original data (bibliographical, museum collections, recent collectings), the high number of observations enable a quantitative analysis. The complete catalogue of captures is deposited at the Centre Suisse de Cartographie de la Faune, CSCF. The Swiss Diplopoda fauna is now rather well known: 127 identified taxa belonging to 6 orders and 18 families. Several systematical obstacles were encountered, mainly due to the purely typological concept of species used in myriapodology. They also indicate the influence on this group of historical factors. For each species the results are discussed and presented in a standard way: a rapid synonymy, bibliographical references of the best descriptions and illustrations, bibliographical references concerning Switzerland, distribution, ecology and phenology, number of observations and distribution map. A qualitative study of the whole fauna, considering populations, is based on the same parameters. Various species-groups are defined after geographical distributions, altitudinal distributions and habitats occupied.

PEDROLI-CHRISTEN, A., 1993. — Faunistique des mille-pattes de Suisse (Diplopoda) / Faunistik der Tausendfüssler der Schweiz (Diplopoda). Neuchâtel, Centre Suisse de Cartographie de la Faune, *Doc. faun. helv.*, **14**, 248 pp.

PEDROLI-CHRISTEN, A., 1996. — Faunistique des mille-pattes de Suisse (Diplopoda) - Faunistik der Tausendfüssler der Schweiz (Diplopoda). *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 281. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

Source : MNHN, Paris

On Myriapod / Insect Interrelationships

Otto KRAUS *& Margarete* KRAUS

Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Martin-Luther-King-Platz 3, D-20146 Hamburg, Germany

ABSTRACT

In the Tracheata (= Antennata), all non-insect taxa are traditionally classified as "Myriapoda". New insights suggest that this may be mistaken. There is good reason to believe that the Chilopoda form the sister taxon of all other Tracheata. Further, a monophyletic unit formed by all progoneate taxa (Symphyla + Pauropoda + Diplopoda) is the most probable sister taxon of the Insecta (= Hexapoda). Hence, Progoneata + Insecta also form a monophylum. This taxon (sister taxon to the chilopods) is called Labiophora. The insects are maintained as a monophyletic unit. There is no reason to separate the Collembola (as "Parainsecta") from the remaining "true" insects. – Available evidence suggests that the basic phylogenetic branching events in the "myriapods" and also in the insects into higher taxa happened very early, presumably in Late Cambrian/ Early Silurian periods.

RÉSUMÉ

Sur les interrelations entre myriapodes et insectes.

Chez les Tracheata ou Antennata, tous les non-insectes sont traditionnellement considérés comme "Myriapoda". De nouvelles données suggèrent que cela pourrait être erroné. Il y a de bonnes raisons de penser que le groupe Chilopoda constitue le taxon-frère de tous les autres Tracheata. D'autre part, l'unité monophylétique formée par tous les Progoneata (Symphyla, Pauropoda et Diplopoda) est le groupe-frère des insectes le plus probable. Désormais, Progoneata + Insecta forment aussi un groupe monophylétique (taxon frère des chilopodes) appelé Labiophora. Les insectes sont maintenus en tant qu'unité monophylétique, car il n'y a pas de raison d'en séparer les collemboles sous le nom de Parainsecta. On peut valablement penser que l'évènement instituant la base phylogénétique des myriapodes et aussi des insectes parmi les autres grands taxons se produisit très tôt, probablement dans la période Cambrien supérieur - Silurien inférieur.

INTRODUCTION

Most authors, and especially textbook authors, continue to maintain the traditional view that myriapods form a taxon, i.e., a monophyletic unit. But various phylogeneticists feel that a group called "Myriapoda" should be regarded as paraphyletic and therefore be abandoned. Controversial discussions of the question which subtaxon of the so-called Myriapoda might be most closly related to the Hexapoda (= Insecta) go back to the early days of POCOCK (1893) and VERHOEFF (e.g., 1910-1914). On the other hand, the concept of the Myriapoda as a taxon was upheld by HENNIG (1969) and also by BOUDREAUX (1987).

There is no reason to question the monophyletic origin of the Tracheata (= Antennata) as a whole, but this assumption should not be based on the presence of tracheae as a character. Convergent evolution of tracheal systems cannot be excluded and is, perhaps, even probable.

KRAUS, O. & KRAUS, M., 1996. — On Myriapod / Insect Interrelationships. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 283-290. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

But there are other, more reliable characters available that should be regarded as autapomorphies of the Tracheata (Fig. 1). For example, the second pair of antennae has been reduced, but its metamere still forms part of the head capsule and is called the intercalary segment. Furthermore, for reasons to be explained below, all tracheates lack a mandibular palpus. In the present paper, we attempt a step-by-step reconstruction of early phylogenetic branching events within the tracheates. In some instances, the fossil record permits estimation of the phylogenetic age of various subtaxa – according to HENNIG's *terminus post quem non* (see e.g., 1969).

MATERIAL AND METHODS

As usual, much of the relevant data is already available and can be derived from previously published papers. Major problems were experienced with reference to the composition of the head capsule and the homology of components of the mouthparts. Specimens preserved in alcohol or BOUIN's fixative were dissected and studied by means of light microscopy (LEITZ interference contrast according to SMITH), and also by scanning electron microscopy (SEM). For light microscopy, chitinous parts were mounted on slides; for embedding, we used HOYER's mixture as this medium has an advantageous light refraction index (for details: see KRAUS, 1984). A camera lucida was used for all drawings.

RESULTS

In this sectio, we deal mainly with uncertainties concerning the composition of the euarthropodean head capsule (see BOUDREAUX, 1987: 120, 121) and investigate various types of mouthparts. The latter part of the investigation is concentrated on the homology of mandibles and on the interpretation of components of the gnathochilarium in Diplopoda and Pauropoda (= Dignatha).

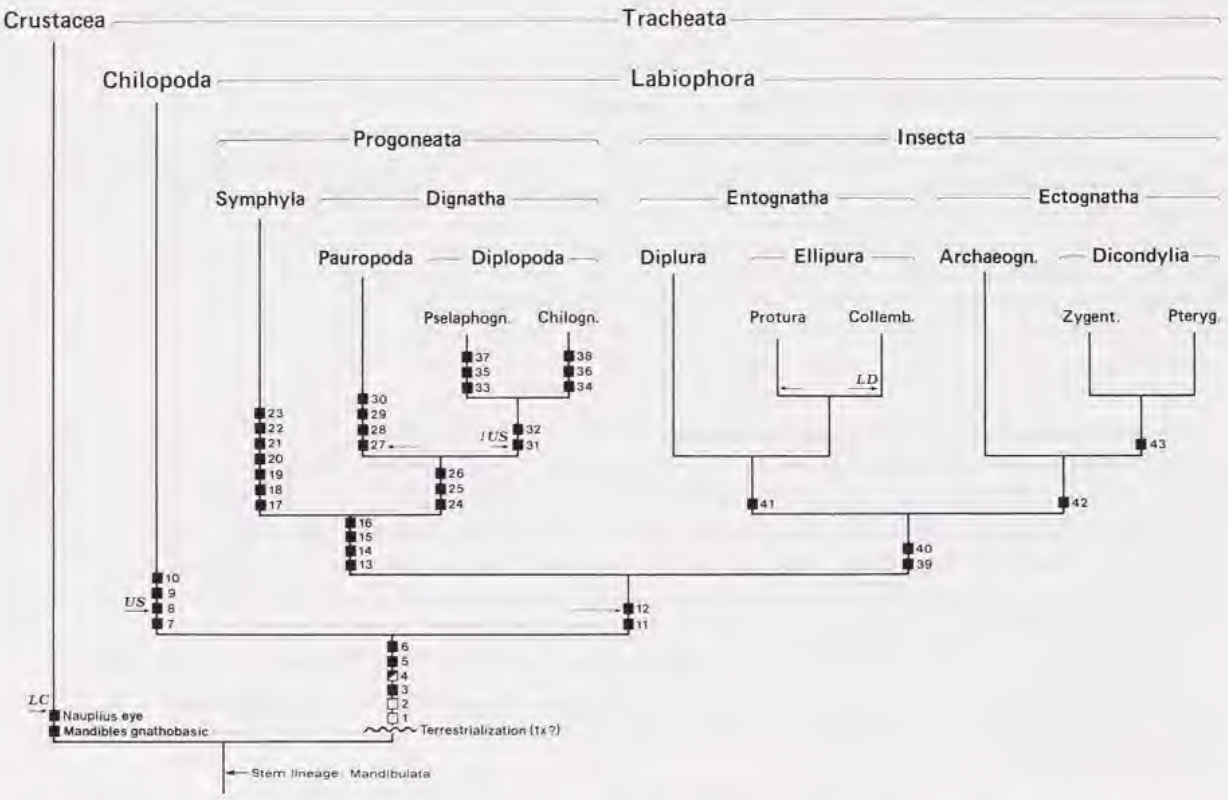


FIG. 1. — Phylogenetic relationships between higher taxa of the Tracheata, their outgroup (Crustacea) included. Arrows indicate age of earliest hitherto known fossils of various groups. — *LC*, Lower Cambrium; *LD*, Lower Devonian; *MD*, Middle Devonian; *US*, Upper Silurian.

Source : MNHN, Paris

Segments of the head capsule

It is now generally accepted that the euarthropodean head capsule includes an acron followed by at least 5 (early fossils), in modern representatives by 6 metameres (LAUTERBACH, 1980a, b; WALOSSECK, 1993: 111). Various authors, however, have believed that the head capsule of the Dignatha is made up of only by 5 metameres. The question arises of whether the regular 6th segment in Pauropoda (TIEGS, 1947: 304) and in at least in Pselaphognatha (Diplopoda) (ATTEMS, 1926: 109) was secondarily excluded from the head capsule *or* whether it had not yet been fully included. A third alternative would be that it *was* and *is* included.

Homology of components of the gnathochilarium

The question of homology is directly concerned with the old problem as to whether the gnathochilarium is made up primarily of the maxillae I *or* by both pairs of appendages, maxillae I and II. VERHOEFF in particular (e.g., 1910-1914), argued that gnathochilaria included two pairs of appendages. This is in contradiction to data derived from ontogenetic studies (DOHLE, 1964, 1980): in the ontogeny of *Glomeris marginata*, the mandibles are followed by only *one* pair of prominent ornaments of appendages. Nonetheless, it remains quite uncertain whether this can be regarded as proof for the assumption that the gnathochilarium does *not* include elements derived from two pairs of appendages.

Pselaphognatha

A study of the gnathochilarium in Pselaphognatha seems to supply the key to solution of the problem: there is no gnathochilarium at all in these diplopods! In *Polyxenus,* the mandibles are followed by two (!) pairs of appendages (Fig. 2a, b). The posterior one shows a very broad and partially bipartite basal plate. This piece bears a pair of appendages. They are equipped with numerous sensillae; we interprete them as leg-like telepodites of the maxillae II. Further, the reader is referred to the presence of traces of articulations between segments of these appendages (Figs. 2a). In a somewhat lateral position, another pair of appendages is present in front of these 2nd maxillae and posterior to the mandibles: these parts still show vestiges of segments. We refer to the position of the duct of the "Putzdrüse" (VERHOEFF's term) and interpret these parts as maxillae I. There is no reason to believe that they might be part of the hypopharynx.

Pauropoda

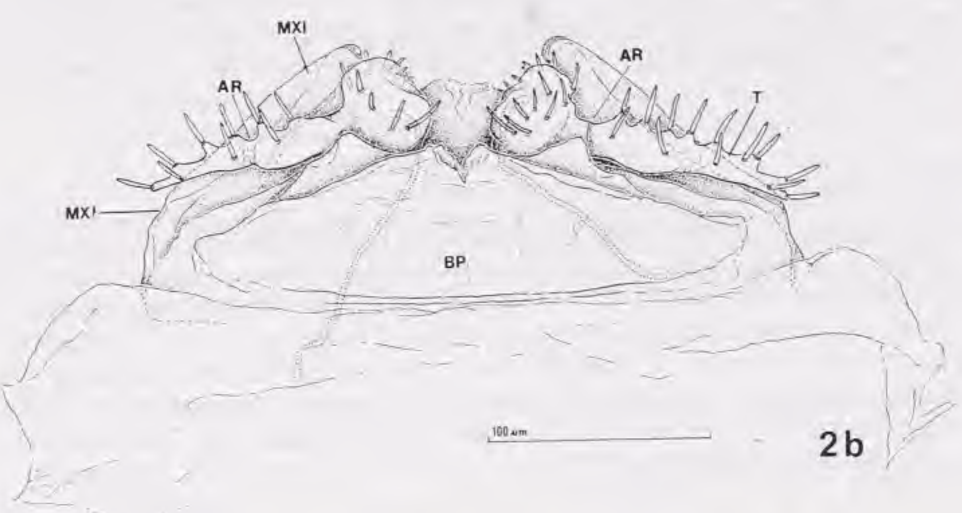
In Pauropods, the head capsule also bears a posterior component which was designated "intermaxillary plate" by TIEGS (1947: 182); this structure does not bear any appendages. In agreement with the arrangement of mouthparts in *Polyxenus*, we interpret the subtriangular plate as representing the maxillae II. In addition, distinct lateral and segmented mouthparts are also present. It was TIEGS (1947), who clearly illustrated their position between the anterior mandibles and the posterior "intermaxillary plate" (see his Fig. 2; also Pl. 3 Fig. 33A). We have studied brachypauropodids and especially Hexamerocerata and can confirm that the position of these paired appendages is between the mandibles and maxillae II (Fig. 3). The obvious interpretation is that they represent the maxillae I. We find it hard to understand how previous authors could invent a pauropodean gnathochilarium (see, e.g., DOHLE 1980: 63, 91).

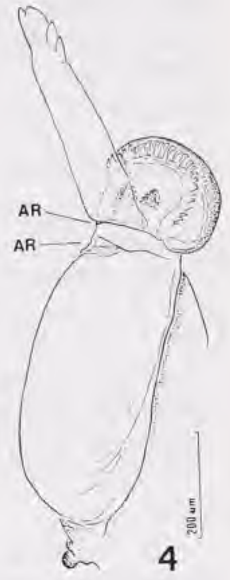
Chilognatha

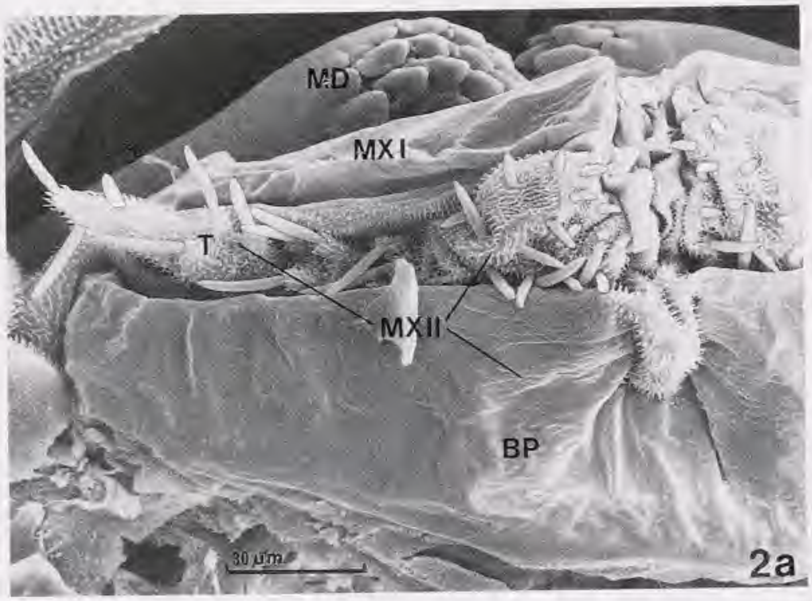
Only in the Chilognatha is a true gnathochilarium present, forming the well-known complex unit (VERHOEFF's "Mundklappe") with median and lateral components. In our view, the lateral elements are homologous with the maxillae I and the median elements with the maxillae II (HILKEN & KRAUS, 1994; KRAUS & KRAUS, 1994). Apparently, this development

Source : MNHN, Paris

is correlated with the acquisition of new food niches, as the Chilognatha feed on larger food particles than the Pselaphognatha. Accordingly, the "perfect" gnathochilarium should be understood in terms of constructional morphology.







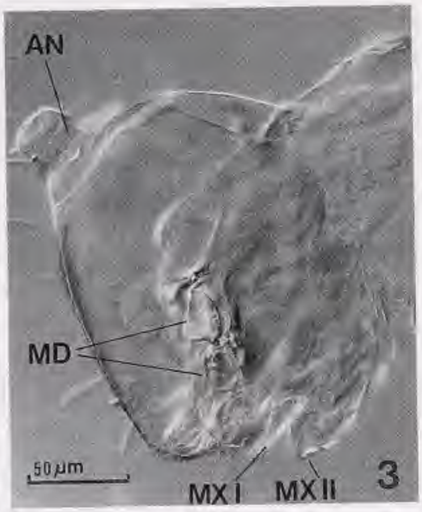


FIG. 2a, b. — *Polyxenus lagurus*, mouthparts. a) SEM-photo, b) drawing. — *AR*, articulations between segments of telopodite, more or less reduced; *BP*, basal plate of maxillae II; *MD*, mandibles, distal part; *MX I*, maxillae I; *MX II*, maxillae II; *T*, telepodites of second maxillae with sensillae.

FIG. 3. — Pauropoda, Hexamerocerata (*Millotauropus silvestrii* Remy, 1953), lateral view of head capsule; *AN*, basis of antenna; *MD*, mandible made up by 3 segments; *MX I*, tip of maxillae I; *MX II*, maxillae II.

FIG. 4. — Archaeognatha (*Trigoniophthalmus alternatus* Silvestri, 1904), telognathic mandible showing vestiges of original articulations (*AR*) between composing segments.

Being fully aware of the fact that this interpretation is in conflict with data derived from ontogeny (DOHLE, e.g., 1980), we argue (i) that there is no other imaginable interpretation of the structures present in postembryonic stages, and (ii) that it is not possible to state definitively

Source : MNHN, Paris

that features do not exist on the grounds that they have not yet seen or may even have remained indiscernible during the course of ontogeny. Another, similar, situation concerning the so-called thoracic segments was described by KRAUS (1990). It is now well established that "true" diplosomites with only one pair of legs really exist among the diplopods (see ENGHOFF, 1993)! Hence, one should ask the reverse question: how is it possible that details remain invisible during the course of ontogeny when they are unquestionably present in postembryonic stages?

In conclusion, there seems to be no reason to doubt that the head capsule in Diplopoda and Pauropoda includes 6 metameres – as in all other extant euarthropods.

Mandibles

In all mandibulates, the appendages of the fourth cephalic metamere have been transformed into mandibles. The crustacean mandible is unquestionably gnathobasic (LAUTERBACH, 1972, 1980a). In the ground pattern of the Crustacea, several distal segments of this pair of appendages are accordingly represented by a palp.

On the other hand, there has been much dispute about whether the mandibles in the Tracheata (= Antennata) are also gnathobasic (LAUTERBACH, 1972) *or* – as MANTON believed (e.g., 1977) – telognathous. Attention is drawn to the various types of segmented mandibles in Chilopoda, Symphyla and Diplopoda (see, e.g. MANTON, 1977); the well-known facts on these can be supplemented. MANTON, who made extensive studies of the head capsule in a species of the machilid genus *Petrobius*, did not realize that segment borders are also clearly visible in the mandibles of the Archaeognatha (Fig. 4). The same is true in the Diplura, at least in representatives of the genus *Dinjapyx* (see MARCUS, 1951). This finding is correlated with the absence of a mandibular palp in all tracheate taxa: telognathous mandibles cannot bear a palp!

We therefore have to conclude that the mandibles in the Mandibulata are homologous as far as they correspond to the appendages of the fourth metamere of the head capsule. Their transformation into jaws happened independently, however: they are gnathobasic in the Crustacea, whereas the appendages were suitably modified in the Tracheata as a whole.

DISCUSSION

Reconstruction of phylogenetic branching

There are convincing reasons for believing that the Tracheata are a monophyletic unit:

Combining our results with previously known details and referring to the hypothesis expressed by the present cladogram (Fig. 1) we argue as set out below:

(1) Arthropodia are generally considered as a key character common to all arthropods. This may be questionable. In addition, it is not absolutely certain whether the transition to terrestrial life and the acquisition of uniramous walking legs (LAUTERBACH, 1980a: 147) took place as early as in the stem lineage of the Tracheata as a whole. See character (24).

(2) As in the ground pattern of the Crustacea, the tracheate maxilla II was primarily leg-like (plesiomorphic condition, maintained in chilopods and also in various Pselaphognatha, e.g., *Polyxenus*).

(3) Teleognathic mandibles are part of the ground pattern of the tracheates.

(4) Paired tarsal claws were regarded by HENNIG (1969: 89) as an autapomorphy of the tracheates. This is highly questionable (see, e.g., diplopodean and ellipuran claws).

(5) An intercalary segment presents the third metamere of the head capsule — without appendages.

(6) No digestive mitgut glands have been maintained in all tracheates. Instead, malpighian tubules were developed. Nonetheless, the homology of these organs needs clarification. At

Source : MNHN, Paris

present, the possibility that malpighian tubules evolved more than once, and hence may not be homologous, cannot be excluded.

Chilopoda

(7) The assumed monophyletic origin of the Chilopoda is strongly supported by the transformation of the appendages of the first postcephalic metamere into "maxillipeds" ("Kieferfüsse").

(8) Chilopods are functionally dignathous: their oral cavity is bordered ventrally by the maxillae I; see character (2).

(9) - (10) Reduction of complex eyes to stemmata; loss of median eyes.

Labiophora

(11) The presence of coxal organs, including styli, is assumed to be an autapomorphy of the adelphotaxon to the chilopods: Labiophora. But DOHLE's critical remarks (1980: 86) should be considered.

(12) According to our interpretation of the diplopodean gnathochilarium and of the mouthparts in the Pauropoda, we conclude that in all subordinated taxa the oral cavity is ventrally bordered by a plate formed by the maxillae II. Hence, all representatives of this major taxon are functionally trignathous. The presence of special dorsal organs during the course of ontogeny may constitute another autapomorphy of this group (for details: see DOHLE, 1980: 88).

Progoneata

(13) The anterior position of the genital opening forms a strong autapomorphy of the taxon Progoneata. The opening is constantly located in front of the fourth pair of legs (but the first pair may be reduced).

(14) All progoneates have trichobothria peculiar to this taxon and unknown in all other terrestrial mandibulates. For details see DOHLE (1980: 72).

(15) In contrast to insects, there are no palpi on the maxillae I. It is assumed that the first maxillae are telognathous in progoneates.

(16) Loss of median eyes.

(17) - (23) Symphyla have many autapomorphies. We will mention only a few: genital opening unpaired; special position of a single pair of tracheal spiracles; complete reduction of median and complex eyes; special structure of maxillae II, total loss of telopodites; spermathecae formed by lateral pockets of the mouth cavity; presence of terminal spinning tubules.

(24) All Dignatha have their tracheal spiracles in a ventral position. Internally, they open into tracheal pockets. They also serve as apodems. Such pockets are also present in pauropods (see REMY, 1953: 37).

(25) Reduction of the first pair of postcephalic appendages. Only pauropods have maintained vestiges: "exsertile vesicles" (see TIEGS, 1947: 182, 249).

(26) Presence of "penes" with openings of the vasal efferentia at the tip.

(27) - (30) Pauropoda have many autapomorphies, including specialized antennae; exsertile vesicles [see (25)]; pseudoculus; maxillae II transformed into an unpaired triangular plate.

Diplopoda

(31) Acquisition of diplopody.

(32) Antennae with four sensory cones on tip.

(33), (35), (37) Complex eyes reduced to 5 isolated ommatidia; gnathochilarium with separate maxillae I and specialized telopodites of maxillae II maintained; soft cuticle with conspicuous groups of hairs.

Source : MNHN, Paris

(34), (36), (38) Complex eyes reduced to stemmata; "complete" gnathochilarium; calcification of cuticle; total loss of trichobothria.

Insecta

As far as insects are concerned, we will only mention the presence of a locomotory thorax made up of the postcephalic metameres I to III (39), and the presence of 11 abdominal metameres in the ground pattern (40). A detailed discussion of phylogenetic branching and relationships within the Insecta (= Hexapoda) would not be appropriate here, the reader is refered to the detailed arguments presented in HENNIG's comprehensive work (1981).

PHYLOGENETIC AGE

The geological age of the earliest fossils presently known is indicated in FIG. 1 (arrows). According to phylogenetic branching, the same age must be inferred to equivalent sister taxa. So the presence of Crustacea as early as in Lower Cambrian times indirectly indicates that representatives of the stem lineage of the Tracheata also existed at this period – irrespective of the fossil record. The most important aspect within the Tracheata is the existence of Diplopoda in deposits of Upper Silurian age. This indicates that previous branching events happened earlier, presumably in Upper Cambrian / Lower Silurian times. It is therefore possible to predict that chilopods are considerably older than the earliest known fossil (*Devonobius delta* Shear, 1988).

ACKNOWLEDGEMENTS

We are indebted to Prof. Dr. W. DUNGER (Görlitz) and Prof. Dr. R. WILLMANN (Göttingen) for critical advice. Dr. U. SCHELLER (Järpas) and Prof. Dr. H. STURM (Hildesheim) kindly helped by providing valuable materials. Karin MEYER's technical support is gratefully acknowledged.

REFERENCES

ATTEMS, K. W., 1926. — Myriapoda. *In* : W. KÜKENTHAL & K. KRUMBACH, *Handbuch der Zoologie*, **4**. *Progoneata, Chilopoda, Insecta*, Berlin und Leipzig, W. de Gruyter & C° : 1-402.

BOUDREAUX, H. B., 1987. — *Arthropod phylogeny, with special reference to insects.* Florida, Malabar, 320 pp.

DOHLE, W., 1964. — Die Embryonalentwicklung von *Glomeris marginata* (Villers) im Vergleich zur Entwicklung anderer Diplopoden. *Zool. Jb. Anat.*, **81** : 241-310.

DOHLE, W., 1980. — Sind die Myriapoden eine monophyletische Gruppe? Eine Diskussion der Verwandtschaftsbeziehungen der Antennaten. *Abh. naturwiss. Ver. Hamburg*, **23** : 45-104.

ENGHOFF, H., 1993. — Haplopodous diplopods: a new type of millipede body construction discovered in cambalopsid juveniles (Diplopoda, Spirostreptida). *Acta zool. Stockholm*, **74** : 257-261.

HENNIG, W., 1969. — *Die Stammesgeschichte der Insekten.* Frankfurt a. M., Kramer, 436 pp.

HENNIG, W., 1981. — *Insect Phylogeny.* New York, John Wiley & Sons, 514 pp.

HILKEN, G. & KRAUS, O., 1994. — Struktur und Homologie der Komponenten des Gnathochilarium der Chilognatha (Tracheata, Diplopoda). *Verh. naturwiss. Ver. Hamburg*, (NF), **34** : 33-50.

KRAUS, O., 1984. — HOYERS Gemisch statt Polyvenyl-Lactophenol. *Mikrokosmos*, **73** : 54-55.

KRAUS, O., 1990. — On the so-called thoracic segments in Diplopoda. *In* : A. MINELLI, *Proc. 7th intern. Congr. Myriapodology.* Leiden, Brill : 63-68.

KRAUS, O. & KRAUS, M., 1994. — Phylogenetic System of the Tracheata (Mandibulata) : on "Myriapoda" - Insecta relationships, phylogenetic age and primary ecological niches. *Verh. naturwiss. Ver. Hamburg*, (NF), **34** : 5-31.

LAUTERBACH, K. E., 1972. — Über die sogenannte Ganzbein-Mandibel der Tracheata, insbesondere der Myriapoda. *Zool. Anz.*, **188** : 145-154.

LAUTERBACH, K. E., 1980a. — Schlüsselereignisse in der Evolution des Grundplans der Mandibulata (Arthropoda). *Abh. naturwiss. Ver. Hamburg*, **23** : 105-161.

LAUTERBACH, K. E., 1980b. — Schlüsselereignisse in der Evolution des Grundplans der Arachnata (Arthropoda). *Abh. naturwiss. Ver. Hamburg*, **23** : 163-327.

MANTON, S. M., 1977. — *The Arthropoda. Habits, functional morphology and evolution.* Oxford, Clarendon Press, 527 pp

MARCUS, H., 1951. — Observaciones morfologicas en *Dinjapyx marcusi. Folia Univ. Cochabamba*, **5** : 83-106.

POCOCK, R. I., 1893. — On the classification of the tracheate Arthropoda. *Zool. Anz.*, **16** : 271-275.

Source : MNHN, Paris

REMY, P. A., 1953. — Description de nouveaux types de Pauropodes: "*Millotauropus*" et "*Rabaudauropus*". *Mém. Inst. scient. Madagascar*, **A8** : 25-41.

TIEGS, O. W., 1947. — The development and affinities of the Pauropoda, based on a study of *Pauropus sylvaticus*. *Quart. J. microscop. Sci.*, **88** : 165-336.

VERHOEFF, K. W., 1910-1914. — *Die Diplopoden Deutschlands, zusammenfassend bearbeitet*. Leipzig, Winter, 482 pp.

WALOSSEK, D., 1993. — The Upper Cambrian *Rehbachiella* and the phylogeny of Brachiopoda and Crustacea. *Fossils & Strata*, **32** : 1-202.

Source : MNHN, Paris

Morphology and Evolution of Circulatory Organs in the Tracheata

Günther PASS

Institut für Zoologie, Universität Wien, Althanstrasse 14, A-1090 Wien, Austria

ABSTRACT

A comprehensive description of the anatomy of the circulatory organs is given from all subtaxa of myriapods, apterygots and some lower Pterygota. In the Chilopoda, a complex vessel system exists which obviously represents a plesiomorphic condition in many respects. According to the most common teaching this system has been widely reduced during the evolution of the Tracheata and in the Hexapoda only the tubular dorsal heart remained. However, in some ancestral insects blood vessels exist in addition which have been partly overlooked so far, but demand special interest from the evolutionary and phylogenetic points of view. One specific trait is a vessel ring caudal to the brain encompassing the gut and connecting the dorsal heart with a short ventral vessel. This structure is found in the Chilopoda, Diplura, Archaeogonata and Zygentoma, but has never been reported in the Pterygota. Special reference is given to the hemolymph supply of longer body appendages, especially the antennae. In general, antennal vessels exist which are considered to be homologous within the Tracheata. In all subtaxa of the myriapods and in the Diplura they originate as arteries from the dorsal vessel. In all other investigated insects they are separated from the latter. At their proximal ends they form ampulla-like enlargements with valved ostia, which communicate with the hemolymph sinus in front of the brain. The connection of the antennal vessels to the dorsal heart in myriapods and Diplura is considered a plesiomorphic state which was apparently lost early in insect phylogeny. Space constraints due to constructional changes in the cephalic capsule are discussed as possible reasons for this loss. In the Archaeogonata and Zygentoma, the ampullae are not pulsatile, and their function is only to funnel hemolymph into the antennal vessels. In higher insects, the ampullae are true forcing pumps as a result of associated muscles ("antenna-hearts"). In different species these muscles diverge with respect to their attachement sites and act either as dilators or as compressors of the ampullae. A derivation of the antenna-heart muscles from pharynx dilators is strongly indicated.

RÉSUMÉ

Morphologie et évolution des organes circulatoires chez les Tracheata.

Une description complète de l'anatomie des organes circulatoires est donnée pour les sous-groupes de myriapodes, d'aptérygotes et de quelques ptérygotes inférieurs. Chez les chilopodes, il existe un réseau complexe de vaisseaux qui représente un état plésiomorphe. Selon les interprétations les plus communément en vigueur, ce système a été largement réduit au cours de l'évolution des antennates et, chez les hexapodes, seul le vaisseau cardiaque dorsal tubulaire s'est maintenu. Cependant, chez certains insectes primitifs, des vaisseaux sanguins existent également, phénomène qui demande à être reconsidéré d'un point de vue évolutionniste et phylogénétique. Un caractère spécifique réside dans le vaisseau caudal annulaire du cerveau qui entoure le tube digestif et relie le cœur dorsal à un court vaisseau ventral. Cette structure se retrouve chez les Chilopoda, Diplura, Archeogonata et Zygentoma,. mais n'a jamais été mise en évidence chez les Pterygota. Il est particulièrement fait référence à l'approvisionnement en hémolymphe nécessaire aux longs appendices du corps, notamment aux antennes. Les vaisseaux antennaires sont considérés comme homologues chez tous les antennates. Dans tous les sous-groupes de myriapodes et chez les diploures, ils apparaissent comme des artères issues

---

PASS, G., 1996.— Morphology and evolution of circulatory organs in the Tracheata. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 291-292. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

du vaisseau dorsal alors que chez tous les autres insectes étudiés ils se séparent de ce dernier. Ils forment à leur extrémité proximale des élargissements en forme d'ampoule, équipés de valvules, qui communiquent, au niveau du cerveau, avec les sinus de l'hémolymphe. La connexion des vaisseaux antennaires avec le cœur dorsal chez les myriapodes et les diploures est considérée comme un caractère plésiomorphe qui a apparemment disparu au cours de la phylogénie des insectes. Les contraintes spatiales dues aux changements survenus dans la construction de la capsule céphalique sont discutées en tant que causes possibles de cette perte. Chez les Archeogonata et les Zygentoma, les structures en ampoule ne sont pas pulsatiles et leur fonction consiste uniquement à permettre à l'hémolymphe de circuler jusqu'aux vaisseaux antennaires. Chez les Insectes supérieurs, elles jouent le rôle de pompes, sortes de "cœurs antennaires" résultant de l'association de muscles. Selon les espèces, ces muscles se distinguent par leurs points d'attache, agissant soit comme dilatateurs, soit comme compresseurs. L'hypothèse d'une évolution de ces muscles du cœur antennaire à partir de dilatateurs du pharynx est fortement suggérée.

Source : MNHN, Paris

Some Problems in the Systematics of the Order Scolopendromorpha (Chilopoda)

Arkady A. SCHILEYKO

Zoological Museum of the Moscow State University, Herzen Street 6, 103009 Moscow K-9, Russia

ABSTRACT

The class Chilopoda ought to be divided into Noto- and Pleurostigmophora in relation to its phylogeny. It is hard to speak about poly- vs. oligomerization as a general pathway in the evolution of the Chilopoda as a whole, chiefly due to an extremely early isolation of the Scutigeromorpha and a polymerous development in the Geophilomorpha. The family Cryptopsidae (Scolopendromorpha) is an unnatural composite taxon because of its polyphyly. This is easily to explain in terms of the theory of biological progress associated in all branches of scolopendromorphs with a transition to a hypogean mode of life.

RÉSUMÉ

Quelques questions de systématique dans l'ordre Scolopendromorpha (Chilopoda).

La classe Chilopoda devrait être divisée, d'après sa phylogénie, en Noto- et Pleurostigmophora. Il est difficile de considérer le contraste "polymétamérisation - oligométamérisation" comme une voie générale de l'évolution de l'ensemble Chilopoda, principalement à cause de l'isolement extrêmement précoce des Scutigeromorpha et du développement "polymétamérique" des Geophilomorpha. La famille Cryptopsidae (Scolopendromorpha) apparaît comme un taxon composite non-naturel à cause de sa polyphylie. Ceci est assez facile à expliquer en théorie par l'association, dans toutes les lignées de scolopendromorphes, d'une évolution biologique et d'une transition vers un mode de vie hypogé.

INTRODUCTION

Chilopod evolution is a subject of active debate (e.g. MANTON, 1952; PRUNESCU, 1965; SHINOHARA, 1970; DOHLE, 1988; SHEAR & BONAMO, 1988). Basically, some studies adhere to oligomerization (= reduction in the number of body segments) as the major evolutionary trend in the Chilopoda, while others document that in terms of polymerization. Systematically, the class has been divided either into Noto- and Pleurostigmophora or Ana- and Epimorpha, dependent on the pattern of allocation of the stigmata and the traits of postembryonic development, respectively. (By the way, is such a character as the type of development (ana- vs. epimorphosis) reliable taxonomically for dividing taxa of so high level?).

However, in addition to new evidence accumulated in the recent years, particularly the discovery of a new extinct chilopod order (SHEAR & BONAMO, 1988), and a new cladistic analysis (DOHLE, 1988), much remains to be clarified, either based on recent results or older literature data.

SCHILEYKO, A. A., 1996. — Some problems in the systematics of the Order Scolopendromorpha (Chilopoda). *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 293-297. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

The main impetus for presenting this preliminary paper lies in the deep interest we can find, among Chilopoda, in the evolution and systematics of the order Scolopendromorpha (e.g. SCHILEYKO, 1992; ZALESSKAJA & SCHILEYKO, 1992).

SYSTEM OF THE SCOLOPENDROMORPHA

At present, the system of ATTEMS (1930) of the centipede order Scolopendromorpha is generally accepted, with such characters as the presence or absence of eyes serving as its basis. The order is divided into two families: Scolopendridae (16 genera with eyes) and Cryptopsidae (12 blind genera) (Fig.1). However, about five years ago, when working with a collection of *Scolopocryptops ferrugineus* (Brölemann, 1919), from Cuba, I found great similarity between *Scolopocryptops*Porat, 1876 and numerous Scolopendridae. In addition, I noted many differences between *Scolopocryptops* and *Cryptops* Leach, 1815 (Fig.1). This provoked the conclusion that Cryptopsidae is possibly a polyphyletic group. In other words, the main reason for revising the system of this order is the apparent polyphyly of the family Cryptopsidae.

To my mind, the Attemsian system seems to reflect the order's eco-morphology rather than phylogeny and fails to explain the allocation within a monophyletic family Cryptopsidae of such quite different representatives as the genera *Scolopocryptops*, *Dinocryptops* Newport, 1844, *Plutonium* Cavanna, 1881 or *Cryptops* (Fig. 1), regardless of the pathway centipede evolution we accept (oligo- vs. polymerization).

I have therefore analyzed all available material from the Zoological Museums of Moscow and St-Petersburg. This amounted to about two thousand specimens from the following genera (Fig. 1): *Theatops* Newport, 1845, *Tonkinodentus* Schileyko, 1992, *Cryptops*, *Paracryptops* Pocock, 1891, *Scolopocryptops*, *Dinocryptops*, *Newportia* (all Cryptopsidae), and *Scolopendra* L., 1758, *Cormocephalus* Newport, 1844, *Asanada* Meinert, 1886, *Otostigmus* Porat, 1876, *Alipes* Imhoff, 1845, *Ethmostigmus* Newport, 1845, *Rhysida* Newport, 1845 (all Scolopendridae).

I have tried to evaluate the maximal number of characters, the main of which are the following (Table 1):

(1) number of spiracles; (2) number of body segments; (3) structure of spiracles; (4) presence of eyes; (5) presence of tooth plates of maxillipede coxosternite; (6) presence of coxopleural pores; (7) presence of coxopleural process; (8) structure and ornament of last legs.

Plesiomorphy is coded by *0*, apomorphy by 1 and serial tranformations by 2 to 4 (Table 1).

TABLE 1. — List of the characters with their evaluation as apomorphy or plesiomorphy.

Characters	Plesiomorphic	Apomorphic
1. Number of spiracle pairs	*19 (0)*	11 (1), 10 (2),9 (3)
2. Number of body segments	*23 (0)*	21 (1)
3. Structure of spiracles	*without flap (0)*	with flap (1)
4. Eyes	*presence (0)*	absence (1)
5. Tooth plates	*presence (0)*	absence (1)
6. Coxopleural pores	*presence (0)*	absence (1)
7. Coxopleural process	*presence (0)*	absence (1)
8. Structure of last legs	*pincer-shaped, without spines (0)*	normal-shaped, with spines (1), leaf-shaped (2), with "saw" (3), many-segmented tarsi (4)

However, I have not attempted a cladogram, because I have not seen representatives of all genera. A cladogram, in this case, would be deficient. Besides, to my mind, the cladistic methods are sometimes not objective, because the choice of characters, the evaluation of degree

Source : MNHN, Paris

of their expression and of their taxonomical importance is rather subjective (same as in the "classic" methods). Because of all this, certainly the set of characters to be analyzed must be extended.

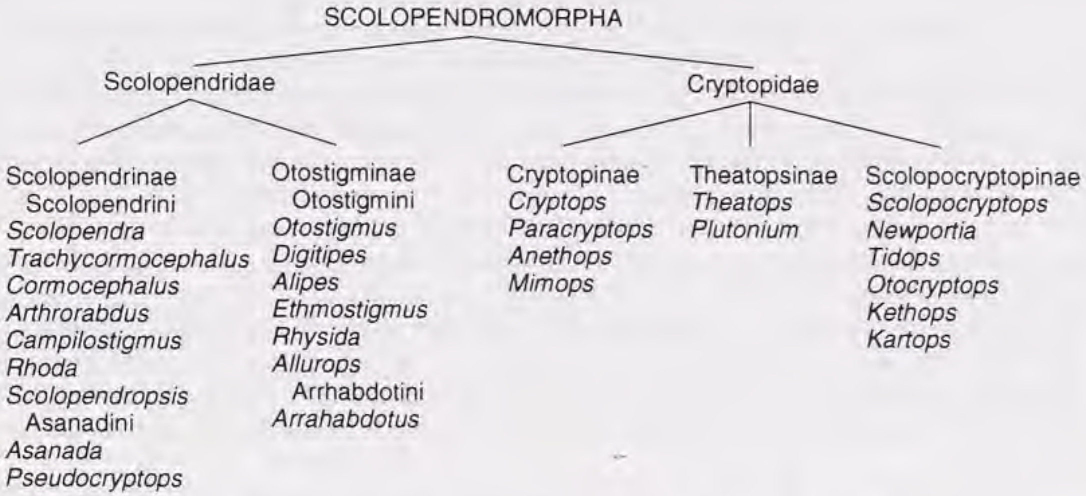


FIG. 1. — System of the Scolopendromorpha after ATTEMS (1930).

A character matrix has been compiled (Table 2). *Plutonium* is a single genus, which I have never personally seen, but I included it in the matrix, because of the great importance of this form for phylogeny of the whole Scolopendromorpha. I analyzed the cardinal character of the system of ATTEMS. To my mind, this character is highly adaptive and not reliable taxonomically. There are numerous examples of eye losses in connection with the transition to a hypogeal mode of life (edaphic and cavernicolous), e.g. in some Lithobiidae centipedes, Atyidae shrimps, Trigonochlamydidae slugs, Characinidae fishes, etc.

Closely related forms with eyes are always present.

The system of ATTEMS is based on a single character. In this case, if one of that two families is polyphyletic, all the system is not reliable. In my opinion, this matrix demonstrates that Cryptopsidae, sensu ATTEMS, is not monophyletic (Table 2).

TABLE 2. — The matrix of the characters.

	Genus	**Characters**							
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Cryptopsidae	*Plutonium*	0	1	0	1	0	0	0	0
	Theatops	3	1	0	1	0	0	1	0
	Tonkinodentus	3	1	0	1	0	0	0	?
	Cryptops	3	1	0	1	1	0	1	3
	Paracryptops	3	1	0	1	1	0	1	3
	Scolopocryptops	1	0	0	1	0	0	0	1
	Otocryptops	2	0	0	1	0	0	0	1
	Newportia	1	0	0	1	0	0	0	4
Scolopendridae	*Scolopendra*	3	1	1	0	0	0	0	1
	Cormocephalus	3	1	1	0	0	0	0	1
	Asanada	3	1	1	0	0	1	1	1
	Otostigmus	3	1	0	0	0	0	0	1
	Alipes	3	1	0	0	0	0	0	2
	Ethmostigmus	2	1	0	0	0	0	0	1
	Rhysida	2	1	0	0	0	0	0	1

Source : MNHN, Paris

In addition, there is a very interesting question about the monotypical genus *Plutonium*, which has 21 body segments with 19 pairs of spiracles, in other words the spiracles are disposed on all body segments, except for the first and the last one (as in Geophilomorpha). As I have already written, the Attemsian system fails to explain the allocation within the family Cryptopsidae of some very morphologically different genera, and at first the allocation of *Plutonium zwierlainii* Cavanna, 1881, regardless of the apo- or plesiomorph type of its homonomity. Some of my ideas about the last problem are as follows.

The evolution of most groups of polymerous invertebrates, which left the soil environment for surface habitats, is known to have undergone oligomerization (Arachnida, Insecta). In my opinion, it is difficult to speak about poly- vs. oligomerization as a general pathway in the evolution of the Chilopoda as a whole, primarily due to an extremely early isolation of the Scutigeromorpha and a polymerous development in the Geophilomorpha. However, it is known that the reduction of spiracles is associated with the development of anisotergy at first, and this takes place in all orders of the Chilopoda which have moved to open habitats.

By the way, a second possible reason for this reduction is apparently connected with a reduced transpiration rate through these structures devoid of epicuticule (KAUFMAN, 1959). Water economy could have become more important during chilopod penetration into arid habitats and regions. The dorso-medial spiracles of Scutigeromorpha are, possibly, the top of evolution of this structure.

But representatives of Geophilomorpha have moved to the hypogean mode of life and have a homonomous and polymerous body without well expressed anisosegmentation. Their polymerization can be easily explained in terms of adaptation to active wormlike movements in a more dense environment. But if the homonomity in Geophilomorpha is an apomorphy, I cannot clearly imagine what their evolutionary pathway was, assuming so because their ancestor had an anisosegmentation. But as an alternative, the Geophilomorpha could have had a homonomous ancestor, and they retained homonomity.

FIG. 2. — The phylogenetic tree of the Chilopoda after SHEAR & BONAMO (1988).

Source : MNHN, Paris

Moreover, the Scolopendromorpha and the Geophilomorpha are closely related groups (PRUNESCU, 1965; DOHLE, 1988; SHEAR & BONAMO, 1988) (Fig. 2) and most probably have a common ancestor. In this case, if body homonomity is a plesiomorphy in the Scolopendromorpha, their ancestor would have had a homonomous body. However, anisotergy would have been absolutely mandatory for groups of centipedes which colonized the soil surface. Anisosegmentation is gradually increasing in the following row: Scolopendromorpha - Craterostigmomorpha - Lithobiomorpha - Scutigeromorpha. Apparently, this fact is due to an increased velocity and manœuvrability while moving and improving the transpiratory system. All these are especially important for predators. I note that this succession is not an evolutionary one, but it is only an attempt to a morpho-functional analysis of anisosegmentation.

CONCLUSIONS

1. So the family Cryptopidae (*sensu* ATTEMS) is probably an unnatural composite taxon, because of its polyphyly. This is easily explicable in terms of the theory of biological progress, associated in all groups of scolopendromorphs with a transition to a hypogean mode of life.

2. If the homonomity is plesiomorphic in the Scolopendromorpha, *Plutonium* is a form most closely related to their common ancestor. Hence, perhaps *Plutonium* deserves not only a family of its own (SCHILEYKO, 1992), but even a suprafamily status, as an absolutely different group.

ACKNOWLEDGMENTS

I am most grateful to the following persons who offered many useful suggestions and improvements to this paper: Dr. A. A. SCHILEYKO, SR, Dr. S. I. GOLOVATCH, Dr M. V. HEPTNER (all Moscow), and Dr. Y. I. STAROBOGATOV (St. Petersburg). Valuable discussions have also been rendered by Dr. H. ENGHOFF (Copenhagen), Dr J. G. E. LEWIS (Taunton), Prof. W. DOHLE (Berlin) and Prof C. PRUNESCU (Bucarest). In addition, I would like extend my deep appreciation to Organising Committee of the 9th Inernational Congress of Myriapodology whose support has enabled me to participate in the congress. A part of this work has been sponsored by the Soros Foundation.

REFERENCES

ATTEMS, G., 1930. — *Myriapoda. 2. Scolopendromorpha. In : Das Tierreich.* Berlin, Walter de Gruyter & Co, 307 pp.

DOHLE, W., 1988. — *Myriapoda and the Ancestry of Insects.* Manchester, Impact Print Services Ltd., 28 pp.

KAUFMAN, Z. S., 1959. — Morphology of spiracles of *Geophilus proximus* C. L. Koch (Chilopoda). *Dokl. AN USSR*, **129** : 698-701. (in Russian).

MANTON, S. M., 1952. — The evolution of Arthropodan locomotory mechanisms. Part 2. General introduction to the locomotory mechanisms of the Arthropoda. *J. Linn. Soc. (Zool.)*, **42** : 93-167.

PRUNESCU, C. C., 1965. — Contribution à l'étude de l'évolution des Chilopodes. *Rev. Roum. Biol. (Zool.)*, **10** : 89-102.

SCHILEYKO, A. A. JR., 1992. — Scolopenders of Viet-Nam and some aspects of the system of Scolopendromorpha (Chilopoda Epimorpha). Part 1. *Arthropoda Selecta*, **1** : 5-19.

SHEAR, W. A. & BONAMO, P. M., 1988. — Devonobiomorpha, a new order of centipedes (Chilopoda) from the middle Devonian of Gilboa, New York State, USA, and the phylogeny of Centiped Orders. *Amer. Mus. Nov.*, **2977** : 1-30.

SHINOHARA, K., 1970. — On the phylogeny of Chilopoda. *Proc. Japan. Soc. Syst. Zool.*, **65** : 35-42.

ZALESSKAJA, N. T. & SCHILEYKO, A. A. JR., 1992. — *The scolopendromorph centipedes of USSR. Moscow*, "Nauka" Publ., 110 pp. (in Russian).

Source : MNHN, Paris

Source : MNHN, Paris

Plesiomorphic and Apomorphic Characters States in the Class Chilopoda

Carol Constantin ***PRUNESCU***

Institute of Biology, 296 Spl. Independentei, RO-79651 Bucarest, Romania

ABSTRACT

The plesiomorphic and apomorphic nature of characters used for a cladistic analysis in the class Chilopoda is taken into account. The plesiomorphic or apomorphic status of the following features are proposed to be discussed here: spiracles and types of respiratory systems, coxal/anal glands (organs), spines of the first article of the female gonopod, male gonopods, testis, genital tract, supernumerary Malpighian tubules.

RÉSUMÉ

États plésiomorphique et apomorphique des caractères dans la classe Chilopoda.

La nature plésiomorphique ou apomorphique de chaque caractère utilisé pour une analyse cladistique des chilopodes est prise en compte. On propose notamment de discuter ici le statut plésiomorphique ou apomorphique des organes suivants : spiracles (stigma) et types de système respiratoire, glandes coxales/anales, gonopodes des femelles, gonopodes des mâles, testicules, tractus génital, tubes de Malpighi supplémentaires.

INTRODUCTION

In 1965 a preliminary phylogenetic tree of Chilopoda was published (PRUNESCU, 1965) already made according to cladistic principles. For the reconstruction of the morphologic characteristics of the primitive chilopods, the primitive morphologic features of representatives of the orders Scutigeromorpha and Lithobiomorpha were selected. This was followed by a synthesis of the research on the anatomy and evolution of the genital system in Chilopoda (PRUNESCU, 1969a), as well as a discussion regarding the place of some atypical chilopods regarding their systematics and evolution (PRUNESCU, 1969b). In 1985, W. DOHLE published a cladistic analysis of the main chilopod groups and suggested a phylogenetic tree resembling that published earlier (PRUNESCU, 1965). A series of morphological features are considered plesiomorphic or apomorphic by DOHLE (1985), not as a result of a critical scientific analysis, but to underline the main resemblances of chilopods ancestors with recent representatives of the subclass Notostigmophora. In in a paper describing the fossil order Devonobiomorpha, SHEAR & BONAMO (1988) dealt with cladistic analysis of several morphologic features treated by DOHLE (1985). Taking into account that some features may have been wrong appreciated by both authors, we considered necessary to reexamine them, as a contribution to the cladistic

PRUNESCU, C. C., 1996. — Plesiomorphic and apomorphic characters states in the class Chilopoda. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 299-306. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

analysis of Chilopoda. A series of features, such as male gonopods, seminal vesicles, supplementary Malpighian tubules were analysed here, for the first time.

CHILOPOD ENVIRONMENT

In our opinion, chilopods originate within the aquatic arthropods. The same opinion is shared by other authors (KRAUS & KRAUS, 1994). The primitive chilopod environment could have been wet or very wet. Most recent chilopods live within a wet environment created by forest soil, deep cracks in rock and by caves. This option satisfies the vital needs of Pleurostigmophora chilopods and offers the natural framework in which these Chilopoda evolved and diversified from the Pleurostigmophora with 15 leg-bearing segments, unequal tergal shields and anamorphic development, to elongated Pleurostigmophora with homonomous secondary segmentation and epimorphic development. We consider the above mentioned wet environment as plesiomorphic for Chilopoda.

The life environment of Notostigmophora which live and hunt in the open air, on rocky walls and open beaches is an apomorphic one, conquered by an ancestral branch of actual Notostigmophora, detached directly from the primitive Pleurostigmophora and having the rank of sister-group with the line from which the present Pleurostigmophora derived. The Notostigmophora preserved most of the plesiomorphic features of the primitive chilopods, but also adapted their metabolism and some of their organs to this different environment.

PAIRED LATERAL SPIRACLES

These structures serve a tracheal system through which gas exchange occurs at the level of the cells of the whole organism. Pleurostigmophora kept a plesiomorphic circulatory system, because their way of life did not imposed a decrease of the blood circulation.

The same type of plesiomorphic circulatory system was also maintained in Notostigmophora. Since S. HAASE (1885), the presence of mid-dorsal spiracle has been considered to have originated in displacement and subsequent median union of the two pleural spiracles. However, tracheal lungs linked by this single median spiracle are paired and are in accordance with the bilateral chilopod organization.

Radical modification of the breathing system in Notostigmophora chilopods results from the gases exchange in "tracheal lungs" between the haemolymph which contains hemocyanin and the oxygenated air, which goes through the tracheae, closed like in a glove finger. The changing of the breathing system in the ancestors of the recent Notostigmophora can be related to the life environment of these chilopods. *Scutigera* hunt almost all their life in the open air, namely in a drier environment than the humid air of leaves and humus. In our opinion, the breathing system in Notostigmophora allowed the inner humidity to be maintained through decreasing water vapour loss at the gas exchange level, in the present apomorphic environment (Fig. 1). This is why we consider that the bilateral spiracles as well as the tracheal breathing system in Pleurostigmophora has plainly plesiomorphic features. Therefore these features can be considered characteristic for the ancestor of the recent chilopods.

The presence of spiracles on leg-bearing segments with large tergites, their absence on leg-bearing segments with small tergites, and the absence of alternation which occur in the successive large tergites on segments VII and VIII, where only the leg-bearing segment VIII has spiracles, argues for the existence of these features in the ancestor of recent Pleurostigmophora. The same strict distribution of the mid-dorsal spiracles is found again in Notostigmophora: the spiracles are present on large tergites of leg-bearing segments inclusive on the unique tergite covering the leg-bearing segments VII and VIII. This homology suggests the presenceof alternation and the lack of alternation as well in the ancestor of Chilopoda (PRUNESCU, 1965).

The problem of lateral spiracles for tracheal breathing and mid-dorsal spiracles for tracheal-lungs breathing must be treated separately from the problem of spiracle distribution on leg-

Source : MNHN, Paris

bearing segments. According to the above argumentation, the tracheal breathing through pleural spiracle is a plesiomorphic feature and the tracheal-lung breathing through mid-dorsal spiracles an apomorphic one. The distribution of spiracles on leg-bearing segments with large tergites in Scutigeromorpha, Lithobiomorpha, Craterostigmomorpha and Scolopendromorpha represents a plesiomorphic feature and the distribution of spiracles on every leg-bearing segments in Geophilomorpha or in the genus *Plutonium* (Scolopendromorpha) is an apomorphic one (PRUNESCU, 1965).

COXAL - ANAL ORGANS

According to ROSENBERG (1982, 1983, 1989), coxal and anal glands are respectively specialized organs for the uptake and release of water vapour and ions from and to the environment. As mentioned above, the plesiomorphic environment of chilopods was a wet one, similar to that now existing under leaves, in humus, etc. These organs are only useful in a wet environment , in order to maintain the water and ion balance of the organism. If the pheromones are eliminated together with the water vapours (LITTLEWOOD, 1983), the plesiomorphic state of these glands is not changed. The lack of these organs in most of the species of Oryidae (ATTEMS, 1929) adapted to dry environments supports the idea of the adaptational loss of these organs in such species. The life style of *Scutigera* , which hunts on stone surfaces in the open air, would not be possible, if the coxal-anal organ were maintained (Fig. 2). Therefore, we consider the coxal-anal gland as a plesiomorphic feature and its absence in Scutigeromorpha as an apomorphic feature. SHEAR & BONAMO (1988) seemed to agree this interpretation but finally consider the absence of such organs as a plesiomorphic feature and their presence as an apomorphic one.

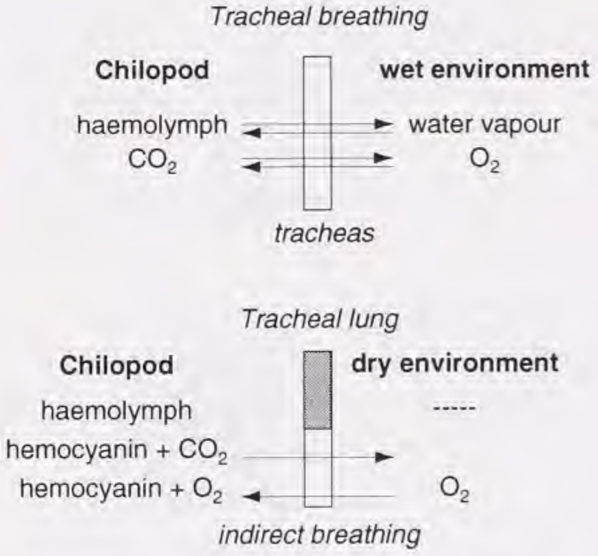


FIG. 1. — Correlation of respiration type with life environment in Chilopoda.

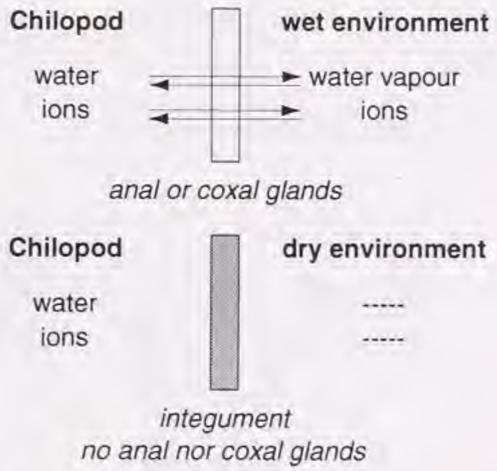


FIG. 2. — Presence and absence of coxal-anal glands in connexion with the life environment of Chilopoda.

In Lithobiomorpha, the coxal glands are located on the last 4 pairs of coxae. We consider this distribution plesiomorphic.

Source : MNHN, Paris

In Scolopendromorpha and Geophilomorpha, coxal glands are distributed on the last pair of coxae, sometimes on the margin of the respective sternite. This reduction of the coxal glands can be considered an apomorphic feature of the first degree.

The older name of "ano-genital capsule" (DOHLE, 1990) seems a misleading name for the structure of the involved organ. Its presence in Craterostigmomorpha only is apomorphic (SHEAR & BONAMO, 1988). In fact, in its two halves, this capsule contains several glands homologous to the coxal glands of other chilopods (unpubl. observations). These glands, leaving the coxae, located in an original organ. The ability of this organ to close firmly or open widely may be linked with the need to con troll water vapour exchange with the environment. A proper name would be the "capsule of coxal-anal glands". This transformation can be considered as an apomorphic feature of the second degree. The lack of coxal glands in Scutigeromorpha can be considered as an apomorphic feature of the third degree.

FEMALE GONOPODS

These organs are highly-modified ambulatory appendages (Fig. 3). As the articles of the ambulatory appendages in Scutigeromorpha and Lithobiomorpha have a large spine (macrosetae) at their distal ends, we consider that the female gonopod, which is characteristic to Lithobiomorpha and has macrosetae, is plesiomorphic.

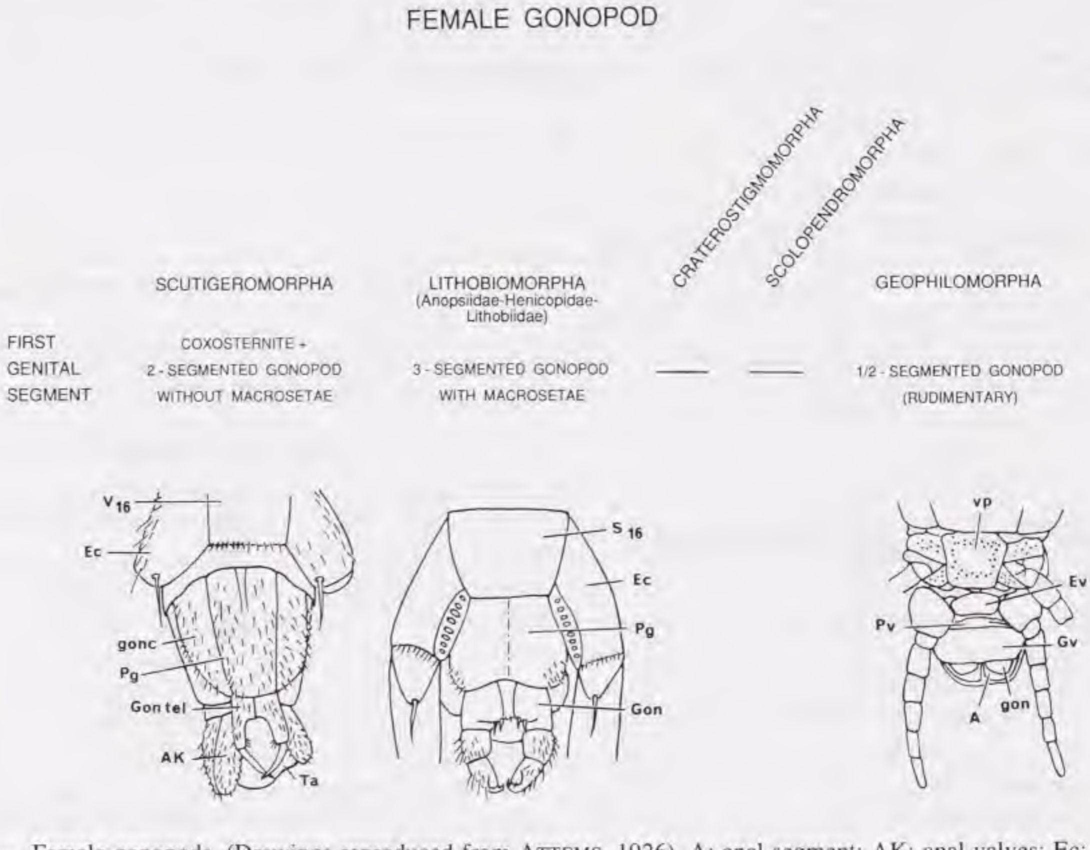


FIG. 3. — Female gonopods. (Drawings reproduced from ATTEMS, 1926). A: anal segment; AK: anal valves; Ec: coxite of the last legs; Ev; sternite of the last leg-bearing segment; gon, Gon: gonopods; gon tel: telopodite of the gonopods; gonc: coxite of the gonopods; Gp: pleurite of the genital segment; gon tel: telopodite of the gonopods; Gv: sternite of the genital segment; Pg, Pv: sternite of the pregenital segment; S_{16} : sternite of the 16th segment; Ta: tergite of the anal segment; V_{16}: sternite of the 16th leg-bearing segment; vp: sternite of the penultimate leg-bearing segment.

Source : MNHN, Paris

The two female gonopods of Lithobiomorpha are firmly separated from one another and formed of three distinct segments, while the female gonopods of Scutigeromorpha comprise two articles, the first one being partly joined (Fig. 3). The female gonopod is a plesiomorphic feature in Lithobiomorpha, an apomorphic one in Scutigeromorpha. Rudimentary female gonopods in Geophilomorpha show a greater degree of apomorphism, of the second degree. The lack of female gonopods in Craterostigmomorpha and Scolopendromorpha is equivalent to an apomorphic feature of the third degree.

MALE GONOPODS

Although the authors of the previous cladistic analysis did not deal with this feature, we think that a review of it is of phylogenetic interest.The most complete male gonopod exists in the representatives of the Henicopidae (Lithobiomorpha). Within this group, the male gonopod consists of 4 distinct segments. In comparison, the male gonopods of Lithobiidae are rudimentary. The male gonopods of Geophilomorpha are formed of two well articulated segments. The male gonopods in Scutigeromorpha are rudimentary but in two pairs (Fig. 4).

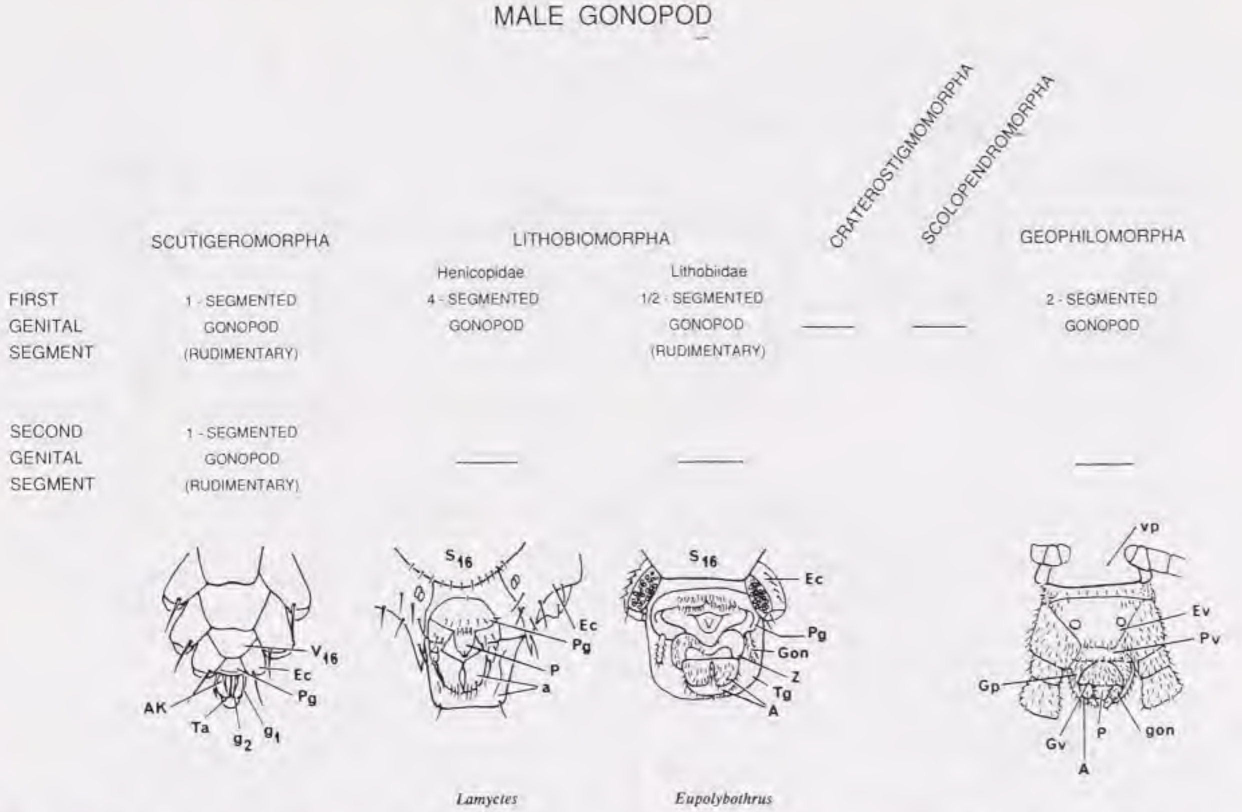


FIG. 4. — Male gonopods. (Drawings reproduced from ATTEMS, 1926). A, a: anal segment; AK: anal valves; Ec: coxite of the last legs; Ev; sternite of the last leg-bearing segment; g_1:pregenital segment of the gonopodes; g_2: rudimentary gonopods of the genital segment; gon, Gon: gonopods; Gp: pleurite of the genital segment; Gv: sternite of the genital segment; p: penis; Pg, Pv: sternite of the pregenital segment; S_{16} : sternite of the 16th segment; Ta: tergite of the anal segment; Tg: tergite of the genital region; V_{16}: sternite of the 16th leg-bearing segment; vp: sternite of the penultimate leg-bearing segment; Z: sternite of the genital segment.

Taking into account their number, they represent a clear plesiomorphic feature of Scutigeromorpha and are apomorphic for all the other chilopods. By the reduction in size and

Source : MNHN, Paris

number of articles, these gonopods are apomorphic. We therefore suggest the separation of "gonopod pairs number" feature from the "gonopod articles number" feature. Thus, any future cladistic analysis will be able to use both features.

The quantification of the "male gonopod articles number" feature could be made as follows:

- Henicopidae: 4 segments = plesiomorphic feature.
- Lithobiidae: rudimentary gonopods = apomorphic feature of the second degree.
- Scutigeromorpha: rudimentary gonopods = apomorpic feature of the second degree.
- Geophilomorpha: biarticulated gonopods = apomorphic feature of the first degree.
- Craterostigmomorpha and Scolopendromorpha: gonopods absent = apomorphic feature of the third degree.

TESTES AND TESTICULAR SYSTEM

In Scutigeromorpha, the male genital system consists of two testes, each formed of a macrotestis and a microtestis (PRUNESCU, 1969c). This structure can also be observed during the larval development (PRUNESCU, 1992b) and is clearly plesiomorphic (Fig. 5).

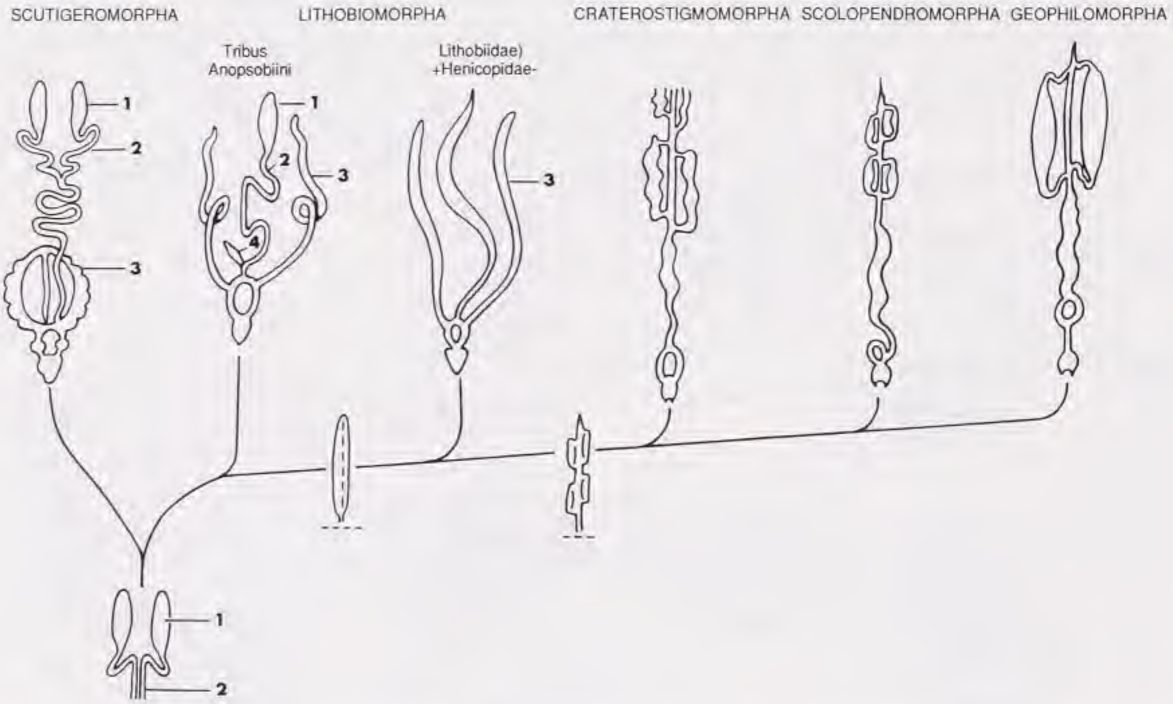


FIG. 5. — Ontogeny and phylogeny of the male genital system in Chilopoda. 1: macrotestis; 2: microtestis; 3: seminal vesicles; 4: undifferenciated rudimentary testis.

In adults of the tribe Anopsobiini (Lithobiomorpha), one testis is undifferentiated and exclusively populated with spermatogonia. The other functional one, consists of macrotestis and microtestis, as in Scutigeromorpha (PRUNESCU & JOHNS, 1969; PRUNESCU, 1992a). This testicular system is apomorphic in the first degree. *Esastigmatobius*, of the Henicopidae (PRUNESCU, MESIBOV & SHINOHARA, this volume) and numerous genera of Lithobiidae (PRUNESCU, 1964) have the testicular system formed of a single testis.

Source : MNHN, Paris

In *Lithobius forficatus*, during larval development, the unique testis results from the joining of two male gonads (BIEGEL, 1922; ZERBIB, 1966). Hence, the single testis in Lithobiidae and perhaps in Henicopidae s. str., is an apomorphic feature of the second degree.

During the larval development of Scolopendromorpha, the two embryonic testis merge to form an unpaired median organ which, by subsequent lateral burgeonings, forms a large deferens duct, to which are linked numerous, pseudometameric, testicular vesicles (HEYMONS, 1901). This is an apomorphic testicular system of the third degree.

Incomplete data for microscopic anatomy show that *Craterostigmus tasmanianus* testicular system structure is similar to that of Scolopendromorpha (PRUNESCU, MESIBOV & SHINOHARA, this volume).

The anatomic data of the testicular system in Geophilomorpha show the presence of two lateral testicular vesicles, linked by a central deferents duct. Thus, Craterostigmomorpha, Scolopendromorpha and Geophilomorpha have an apomorphic testicular system of the third degree. According to the present state of knowledge, we cannot differentiate a distinct apomorphic degree between the testicular system in Geophilomorpha with that of Scolopendromorpha.

MALE GENITAL TRACT

The male genital tract is constituted by the genital organs between the testes and the genital atrium. This anatomical structure follows a clear evolution simplification.

In Scutigeromorpha several organs play an important role in the deposition, maturation and preservation of spermatozoa. We consider that this is a plesiomorphic feature. Of this very complex and histologically varied anatomic system, only two elongated tubes are retained in Lithobiomorpha. They are named seminal vesicles and have the same role as the similar organs of Scutigeromorpha. This is an apomorphic situation of the first degree.

In Craterostigmomorpha, Scolopendromorpha and Geophilomorpha orders, the seminal vesicles are absent, their function being taken over by the posterior half of the very expended deferens duct. In this duct, the spermatozoa are deposited and the spermatophores formed (JANGI, 1956). This can be considered as an apomorphic feature of the second degree.

SUPERNUMERARY MALPIGHIAN TUBULES

Only two Malpighian tubules were known to be present in all chilopod groups (LEWIS, 1981).

In *Scutigera coleoptrata* we found a supplementary pair of Malpighian tubules, which have dorso-ventral insertion, at the level of the junction of the mid-gut with the hind-gut.

In *Craterostigmus tasmanianus* we found only one supplementary Malpighian tubule, which has a medio-dorsal insertion at the same area of the intestine, and which is directed towards the posterior region of the body (see PRUNESCU & PRUNESCU, this volume).

The presence of two supplementary Malpighian tubules in *Scutigera coleoptrata* suggests they are plesiomorphic. As a rule, in Chilopoda, the evolution presents a tendancy to simplify the features of different systems or organs. So, the absence of supernumerary Malpighian tubules in Lithobiomorpha is an apomorphic feature of the second degree. The disappearance of the ventral supernumerary tubule in *Craterostigmus tasmanianus* represents an apomorphic feature of the third degree, while the presence of the dorsal supernumerary tubule represents a plesiomorphic one. The absence of any supernumerary Malpighian tubule in Scolopendromorpha and Geophilomorpha represents an apomorphic feature of the second degree, distinct from the apomorphic feature of the second degree in Lithobiomorpha, which was realized by its own evolutive line.

Source : MNHN, Paris

REFERENCES

ATTEMS, C. , 1926. — Myriopoda. *In* : W. KÜKENTHAL & T. KRUMBACH, *Handbuch der Zoologie,* **4**, *Progoneata, Chilopoda, Insecta*, Berlin & Leipzig, W. de Gruyter & C° : 1-402.

ATTEMS, C., 1929. — Myriapoda 1. Geophilomorpha. *In* : F. E. SCHULZE & W. KÜKENTHAL, *Das Tierreich*, **52**. Berlin & Leipzig, W. De Gruyter & C° : 1-388.

BIEGEL, J., 1922. — Beiträge zur Morphologie und Entwicklung Geschichte des Herzens bei *Lithobius forficatus* (L.). *Rev. Suisse Zool.*, **29** : 444-480.

DOHLE, W., 1985. — Phylogenetic pathways in the Chilopoda. *Bijdr. Dierk.*, **55** : 55-66.

DOHLE, W., 1990. — Some observations on morphology and affinities of *Craterostigmus tasmanianus* (Chilopoda). *In* : A. MINELLI, *Proc. 7th Intern. Congr. Myriapodology*, Leiden, E. J. Brill : 69-79.

HAASE, E., 1885. — Zur Morphologie der Chilopoden. *Zool. Anz.*, **8,** n° 216 : 693-696.

HEYMONS, R., 1901. — Entwicklungsgeschichte der Scolopender. *Biblioth. Zoologica Chun.*, **33** : 82-196.

JANGI, B. S., 1956. — The reproductive system in the male of the centipede *Scolopendra morsitans*. *Linn. Proc. Zool. Soc. Lond.*, **127** : 145-159.

KRAUS, O. & KRAUS, M., 1994. — Phylogenetic System of the Tracheata (Mandibulata): on "Myriapoda" - Insecta relationships, phylogenetic age and primary ecological niches. *Verh. naturwiss. Ver. Hamburg*, (NF), **34** : 5-31.

LEWIS, J. G. E., 1981. — *The biology of Centipedes.* Cambridge, Cambridge Univ. Press, 475 pp.

LITTLEWOOD, P. M. H., 1983. — Fine structure and function of the coxal glands of lithobiomorph centipedes: *Lithobius forficatus* and *L. crassipes* (Chilopoda, Lithobiidae). *J. Morphol.*, **177** : 157-159.

PRUNESCU, C. C., 1964. — Anatomie microscopique du système génital mâle des Lithobiidés. *Rev. Roum. Biol. (Zool.)*, **9** : 101-104.

PRUNESCU, C. C., 1965. — Contribution à l'étude de l'évolution des Chilopodes. *Rev. Roum. Biol. (Zool.)*, **10** : 89-102.

PRUNESCU, C. C., 1969a. — Considérations sur l'évolution du système génital des Chilopodes. *Bull. Mus. natl. Hist. nat., Paris*, **41, suppl. 2** : 108-111.

PRUNESCU, C. C., 1969b. — Quelle est la place occupée par *Cermatobius*, *Craterostigmus* et *Plutonium* dans la phylogénie des Chilopodes? *Bull. Mus. natl. Hist. nat. Paris*, **41, suppl. 2** : 112-115.

PRUNESCU, C. C., 1969c. — Le système génital mâle de *S. coleoptrata*, (Notostigmophora, Chilopoda). *Rev. Roum. Biol. (Zool.)*, **14** : 185-190.

PRUNESCU, C. C., 1992a. — The genital system in *Dichelobius* (Anopsobiidae, Lithobiomorpha, Chilopoda), *Ber. nat.-med Verein Innsbruck,* **suppl. 10** : 87-91.

PRUNESCU, C. C., 1992b. — The beginning of double spermatogenesis in *Scutigera coleoptrata*. *Ber. nat-med Verein Innsbruck*, **Suppl. 10** : 93-97.

PRUNESCU, C. C. & JOHNS, M., 1969. — An embryonic gonad in adult males of *Anopsobius neozelandicus* Silv. (Chilopoda). *Rev. Roum. Biol. (Zool.)*, **14** : 407-409.

ROSENBERG, J., 1982. — Coxal organs in Geophilomorpha (Chilopoda), organization and fine structure of the transporting epithelium. *Zoomorphology*, **100** : 107-120.

ROSENBERG, J., 1983a. — Coxal organs of *L. forficatus* (Myriapoda, Chilopoda). Fine structural investigation with special reference to the transport epithelium. *Cell Tissue Res.*, 230 : 421-430.

ROSENBERG, J., 1983b. — Coxal organs in Scolopendromorpha (Chilopoda). Topography, organization, fine structure and signification in Centipedes. *Zool. Jb. Anat.*, **110** : 383-393.

ROSENBERG, J., 1989. — A key to the middle European Centipedes (Geophilomorpha) based on the coxal pores. *Acts Biol. Benrodis*, *1988*,**1** : 133-141.

SHEAR, W. A. & BONAMO P., 1988. — Devonobiomorpha, a new order of Centipeds (Chilopoda) from the middle Devonian of Gilboa, New York State, USA, and phylogeny of centiped orders. *Am. Museum Novitates*, **2927** : 1-30.

ZERBIB, C. W., 1966. — Etude descriptive et expérimentale de la différentiation de l'appareil génital du Myriapode Chilopode *Lithobius forficatus* (L.). *Bull. Soc. zool. France*, **91** : 203-216.

Source : MNHN, Paris

A Preliminary Study on Phylogeny and Biogeography of the Family Paracortinidae (Myriapoda: Callipodida): a Cladistic Analysis

Daqing WANG

Department of Invertebrates, Institute of Zoology, Academia Sinica, Beijing 100080, P.R. China

ABSTRACT

The phylogeny and biogeography of a millipede family (Paracortinidae, fam. nov.) are preliminary examined by using a cladistic analysis. One of the 35 most parsimonious trees (cladograms), which also has the lowest (best) F value, is congruent with the scheme of evolution proposed by WANG & ZHANG (1993) from systematical analysis. Yunnan millipede *R. stimulus* is the sister group of all other extant Paracortinae. The other clade has the three Tibet species, *A. viriosum*, *A. serratum* and *A. carinatum* as the sister group of three Sichuan species, *P. voluta*, *P. leptoclada* and *R. thallinus*. The biogeography is inferred from the most parsimonious phylogenetic hypothesis of millipedes. The ancestral millipede in Yunnan moved first northward and diverged into two stocks. Subsequently, one of them moved eastward first and then vicariated into an eastern population and a western population. The another moved eastward and then separated into a western population and an eastern population. Some geological events are discussed for their possible effects in the formation of the present pattern of millipede distribution.

RÉSUMÉ

Phylogénie et biogéographie de la famille Paracortinidae (Diplopoda : Callipodida) : analyse cladistique préliminaire.

La phylogénie et la biogéographie d'une famille de diplopodes (Paracortinidae, fam. nov.) font l'objet d'une étude préliminaire à l'aide d'une analyse cladistique. L'un des 35 arbres les plus parcimonieux, qui présente la valeur de F la plus basse (la meilleure?), est congruent avec le bilan évolutif proposé par WANG & ZHANG (1993) à partir d'une étude systématique. Le diplopode du Yunnan *R. stimulus* est le groupe-frère de tous les autres Paracortinae. Trois espèces du Tibet, *A. viriosum*, *A. serratum* et *A. carinatum* constituent le groupe-frère de trois espèces du Sichuan, *P. voluta*, *P. leptoclada* and *R. thallinus*. Ils sont monophylétiques et constituent une trichotomie avec l'espèce du Yunnan, *R. stimulus*. La biogéographie est déduite de l'hypothèse de plus grande parcimonie pour les diplopodes. L'ancêtre des diplopodes du Yunnan s'est déplacé tout d'abord vers le nord et s'est divisé en deux stocks. Ultérieurement, l'un d'entre eux s'est d'abord déplacé vers l'est, puis a constitué une vicariance entre une population orientale et une population occidentale. L'autre s'est alors déplacé vers l'est et s'est séparé entre une population occidentale et une population orientale. La possibilité d'une influence d'évènements géologiques dans la formation des modalités actuelles de la répartition des diplopodes est discutée.

INTRODUCTION

Cladistic analysis is a systematic method that attempts to discover genealogical (phylogenetic) relationships between taxa (HENNIG, 1966; WILEY, 1981). Since a detailed

---

WANG, D., 1996. — A preliminary study on phylogeny and biogeography of the family Paracortinidae (Myriapoda: Callipodida): a cladistic analysis. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 307-311. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

phylogenetic hypothesis for a group of organisms can and should serve as a basis for inferring the biogeographic history (HENNIG, 1966; BRUNDIN, 1966; NELSON & PLATNICK, 1981; HUMPHRIES & PARENTI, 1986), I have used this approach to study the phylogenetic relationships and biogeography of some millipedes (Callipodida: Paracortinidae). This paper preliminary reports some of these results, that will be precised in future works.

CHARACTER ANALYSIS

I chose the species of the genus *Eurygyrus* as the outgroup. From the analysis of morphology, the species of the genus *Eurygyrus* are close to the family Paracortinidae in affinities and the latter is rather ancient. This result can be derived from the descriptions of the morphological and diagnostic characters of the seven species of paracortinids. The morphological difference and diagnostic characters of the seven species were described in the paper, including the following ten characters listed in Table 1 (WANG & ZHANG, 1993). Table 1 gives the coding of morphological characters proposed for the paracortinid species, and Table 2 shows the matrix of the character states in the seven extant species of paracortinid millipedes. The branch and bound algorithm from the phylogenetic computer package PAUP 2.4.1, which guarantees the finding of all the most parsimonious trees, was used in this preliminary analysis.

TABLE 1. — Coding of the morphological characters for the seven paracortinid species.

Character	States of character: (code)
1. ratio of 4th-6th segments antennae	0: 1:1 1: < 1:1
2. process of 7th pair of legs in male	0: none 1: two
3. body color	0: dark brown 1: slight yellow
4. size of crests on collum	0: small and short 1: large and long
5. shape of collum edges	0: arch-shaped 1: parallel
6. shape of the median sclerite of hypoproct	0: rectangle 1: square
7. shape of eyes	0: ladder-shaped 1: triangular
8. gonopods	0: protrude from body 1: include in the body
9. concavity on front of head	0: deep 1: none
10. beak-shaped process in front head	0: none 1: large one

TABLE 2. — Matrix of character states in the seven new species of paracortinid millipedes. (Outgroup = genus *Eurygyrus*).

species	coding of characters									
	1	2	3	4	5	6	7	8	9	10
R. stimulus	0	0	1	0	0	0	0	0	0	0
A. carinatum	1	0	0	0	0	0	0	1	1	0
A. viriosum	0	0	0	1	1	0	0	1	1	0
R. thallinus	0	0	0	0	0	0	0	1	1	0
P. voluta	0	0	0	0	0	1	0	1	0	1
A. serratum	0	1	0	0	1	0	0	1	1	0
P. leptoclada	0	1	0	0	0	1	0	1	0	1
OUTGROUP	0	0	0	0	0	0	0	0	0	0

Source : MNHN, Paris

PHYLOGENY

A large number of trees (cladograms) was obtained, 35 in total, all with a consistency index of 0.636. The F value of these most parsimonious trees ranged from 0.155 to 0.611. However, there is only one tree with the lowest (best) F value, shown in Figure 1. BROOKS *et al.* (1986) suggested that the lower the F-ratio (= F value), the greater the degree of historical constraint on the data. In this regard, the tree with the lowest F value (Fig. 1) should exhibit the highest degree of congruence with the hypothesis of paracortinid evolution.

The phylogenetic hypothesis indicates that the Yunnan species, *R. stimulus* is the sister group of all other extant paracortinids. The species *A. carinatum* is the sister group of *A. viriosum* and *A. serratum*. The species *R. thallinus* is the sister group of *P. leptoclada* and *P. voluta*. Three Tibet species, *A. viriosum*, *A. serratum* and *A. carinatum*, and the three Sichuan species, *P. leptoclada*, *P. voluta* and *R. thallinus* are monophyletic and constitute the sister group that forms a trichotomy.

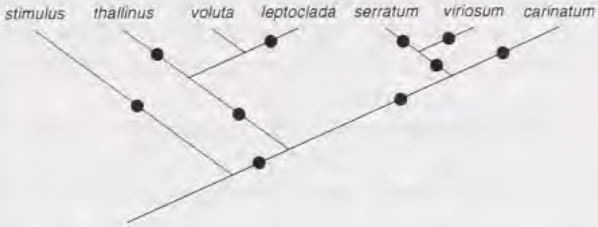


FIG. 1. — Cladogram showing hypothesized relationships among species of paracortinids.

Based on the fact that the setal patterns of Callipodida not only vary distinctly among different genera, but to a large extent correspond closely to groupings made on the basis of gonopod structure, (HOFFMAN, 1972), I propose the classification of the genera of the family Paracortinidae as follows:

g. Paracortina: Paracortina leptoclada, Paracortina voluta
g. Relictus: Relictus stimulus, Relictus thallinus
g. Altum: Altum viriosum, Altum carinatum, Altum serratum

Comparing this classification with the hypothesis, the only difference between them is the placement of the species *R. thallinus*, but the rest show the highest degree of congruence. This point would strongly support the cladogram shown in Figure 1. As for the difference, it is an interesting question and further study is needed.

BIOGEOGRAPHY

According to the principle of vicariance biogeography (NELSON & PLATNICK 1981; HUMPHRIES & PARENTI, 1986), a pattern of spatial distribution attained by the paracortinids can be deduced from the phylogenetic hypothesis. The area summary cladogram in Figure 2 illustrates how the present pattern of paracortinid distribution was attained.

According to the progression rule of HENNIG (1966), it implies that the ancestral paracortinid, residing in Yunnan, diverged into two lineages. One gave rise to the modern Zhongdian (Yunnan) species (*stimulus*, Fig. 2) , and the other formed the species A (Fig. 2), which is the ancestor of all other extant paracortinid species. Species A migrated northward and then vicariated into two populations: the western population (B, Fig. 2) whose descendants later occupied Mongkang and Deqin (Tibet), and the eastern population (C, Fig. 2), whose descendants gave rise to all the paracortinids in Yiajang and

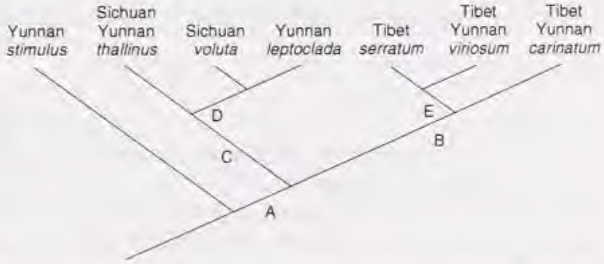


FIG. 2. — Area summary cladogram of paracortinids with ancestral species (A - E).

Source : MNHN, Paris

Batang (Sichuan). Species B migrated northward and then separated into the modern species *carinatum* and a species E, the ancestor of extant two Tibet species *serratum* and *viriosum*. Species C expanded eastward and diverged into the extant species *thallinus* and a species D, which is the ancestor of the extant two Sichuan species, *voluta* and *leptoclada*.

Geological events that cause fragmentation of a continuous ancestral distribution are considered the major reasons of distribution pattern formation (NELSON & PLATNICK, 1981). Although not all vicariant events are identifiable at present, the following are known geological events that could have produced the present pattern of paracortinid distribution.

Mong Kang and Deqin (Tibet) lie in a strip of land between two large rivers: the western Lancang River and the eastern Jinsha River. Batang and Yajiang (Sichuan) face the Jinsha River to the the west and the Yalong River to the the east. The three rivers flow rapidly so that it is not possible for paracortinids to cross. In other words, this vicariance took place before the emergence of the three large rivers.

The formation of the three rivers is the result of elevation of the Hengduan Mountains in the later Tertiary (PHYSIOGRAPHY OF CHINA, 1985). The fossil members of the order Callipodida indicate that callipodoids at least were widespread in Western Asia and North America (HOFFMAN, 1969). That is to say that it is very possible for paracortinids to migrate and diverge before the formation of the three rivers. The Tibetan species *leptoclada* and Sichuan species *carinatum* are being in Zhongdian (Yunnan) strongly support this idea.

The early paracortinid ancestor of Yunnan (Zhongdian) migrated northward before the Tertiary, then diverged into extant species *stimulus* and species A. Species A vicariated into western and eastern populations: Tibet species B and Sichuan species. Because of the emergence of the Langcang River and the Jinsha River, in the Tertiary, species B was separated, and then diverged into the extant species *thallinus* and a species D. The latter is the ancestor of species *voluta* and *leptoclada* . Species C was also separated in the later Tertiary because of the formation of the Jinsha River and the Yalong River. Then it diverged into the extant species *carinatum* and the species E, which is the ancestor of two species, *serratum* and *viriosum*.

CONCLUSION

The phylogenetic hypothesis of paracortinids (FIG. 1) presented in this work is the most parsimonious scheme derived from the cladistic analysis. It is congruent with the scheme of evolution proposed by WANG & ZHANG (1993). The vicariance model proposed for paracortinid biogeography is based on the adopted most parsimonious tree that shows congruence with the extant pattern of spatial distribution attained by paracortinids. The model interprets that (1) paracortinids arose in Zhongdian, Yunnan; (2) migrated northward before the Tertiary and then diverged westward and eastward; (3) because of the formation of three large rivers in the Tertiary, western and eastern populations were separated and then diverged into the extant paracortinids.

Nevertheless, it should be noted that the biogeographic hypothesis presented in this paper is to be considered as preliminary. More complete analysis will be proposed in future works.

ACKNOWLEDGMENTS

I wish to express my sincere thanks to Prof. HO Jushey at the California State University (USA) for permitting me to use his computer package PAUP 2.4.1 for cladistic analysis. And I am grateful to Ms. WANG Xiaowei and Mr. WANG Jian at the Institute of Zoology, Academia Sinica, for their spending much time on the computer runs. In particular, I thank Dr J.J. GEOFFROY (editor) and unkown-names referees for their critical reading, comments and suggestions on this preliminary paper.

Source : MNHN, Paris

REFERENCES

BROOKS, D. R., GRADY, R. T. O. & WILEY. E. O., 1986. — A measure of the information content of phylogenetic trees, and its use as an optimality criterion. *Syst. Zool.*, **35** : 571-581.

BRUNDIN, L., 1966. — Transantarctic relationships and their significance, as evidenced by chironomid midges. *Kungl. Svenska Vetenskap. Handl.*, **11**. : 1-472.

HENNIG, W., 1966. — *Phylogenetic systematics*. Urbana, Univ. Illinois Press. 263 pp.

HOFFMAN, R. L., 1969. — Myriapoda, exclusive of Insecta. *In* : *Treatise on Paleontology. Part R, Arthropoda 4*, **2** : 571-606.

HOFFMAN, R. L., 1972. — Studies on Anatolian callipoid Diplopoda. *Mitt. Hamburg Zool. Mus. Inst.*, **69** : 81-108.

HUMPHRIES, C. J. & PARENTI, L. R., 1986. — *Cladistic biogeography*. Oxford, Clarendon Press. 98 pp.

NELSON, G., & PLATNICK, N., 1981. — *Systematics and Biogeography, cladistics and vicariance*. New-York, Columbia Univ. Press. 567 pp.

PHYSIOGRAPHY OF CHINA, 1985. — Edited by the Committee of "Physiography of China", Beijing, Academia Sinica. Sci. Press : 13-49.

WILEY, E. O., 1981. — *Phylogenetics: The theory and pratice of phylogenetic systematics*. New-York, J. Wiley & Sons. 439 pp.

WANG, D. & ZHANG, C. Z., — 1993. — A new family of millipeds (Diplopoda: Callipodida) from Southwestern China. *Peking Nat. Hist. Mus., Mem.*, **53** : 375-389.

Source : MNHN, Paris

Source : MNHN, Paris

The Penis as a Phylogenetic Character in the Millipede Family Julidae

Henrik ENGHOFF

Zoologisk Museum, Københavns Universitetsparken 15, DK-2100 København, Danmark

ABSTRACT

The double penis provides useful characters for analysing phylogenetic relationships within the family Julidae. In his treatment of the Diplopoda in Bronn"s *Klassen und Ordnungen des Tierreichs*, VERHOEFF (1926-32) noted the difference between *Pachyiulus* and the other Julids examined. Study of numerous julid genera has confirmed this distinction: All Pachyiulini have one type of penis - other julids (with a few, obviously secondary, exceptions) have another type. The pachyiuline type is taken to be primitive, being more similar to penis types found in related families. The other type thus constitutes a potential synapomorphy for all Julidae except Pachyiulini. The non-pachyiuline penis type shows several further modifications which probably qualify as synapomorphies at lower hierarchical levels. Thus, all Paectophyllini and Calyptophyllini have an unusually stout and sclerotized penis, and all species of *Anaulaciulus* have the terminal lobes of the penis particularly long.

RÉSUMÉ

Le pénis comme caractère phylogénétique dans la famille Julidae (Diplopoda).

Dans la famille Julidae, le double pénis fournit des caractères très utiles pour l'analyse des relations phylogénétiques. Dans son traité des diplopodes dans le Bronn's *Klassen und Ordnungen des Tierreichs*, VERHOEFF (1926-32) notait déjà la différence entre *Pachyiulus* et les autres julides qu'il avait observés. L'étude de nombreux genres de julides a confirmé cette distinction : tous les Pachyiulini possèdent un même type de pénis alors que les autres julides (sauf quelques exceptions traduisant à l'évidence des modifications secondaires) présentent un autre type. Le type de pénis des Pachyiulini est considéré comme primitif (plésiomorphe) à cause de sa similitude avec le type de pénis des familles phylogénétiquement voisines. L'autre type constitue une synapomorphie potentielle pour tous les Julidae sauf les Pachyiulini. Plusieurs modifications du type de pénis non-Pachyiulini constituent probablement des synapomorphies établies à des niveaux inférieurs. Par exemple, tous les Paectophyllini et les Calyptophyllini possèdent un pénis exceptionnellement robuste et sclérifié, et toutes les espèces du genre *Anaulaciulus* présentent des lobes péniens terminaux particulièrement longs.

INTRODUCTION

As in most other millipede groups, the taxonomy of the large Palearctic family Julidae relies heavily on the gonopods. This is true both on species level and on higher levels. Recent studies have demonstrated, however, that certain species in some julid genera cannot be distinguished on gonopodal characters (see, e.g., ENGHOFF, 1987, 1992), and also that the phylogenetic relationships of julidan families cannot be satisfactorily analysed by means of gonopodal characters alone (ENGHOFF, 1981, 1991). At the intermediate level, the only recent

ENGHOFF, H., 1996. — The penis as a phylogenetic character in the millipede family Julidae. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 313-326. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

attempt at a phylogenetic analysis of the tribes within the Julidae is that of READ (1990) which relies very much on gonopods.

The present study focuses on another part of the male sexual system, namely the penis, and on the phylogenetic significance of the morphological variants found within this family.

In those millipedes which do have a penis, it is a single or double tube situated behind the second pair of legs. The penis is used to load the proper copulatory organs, the gonopods, with sperm (HAACKER & FUCHS, 1970).

Although the penis has received relatively little attention from diplopodologists, it is noteworthy that the higher classification of the Diplopoda by COOK (1895) to some extent was based on the nature of the penis (or rather: of the male gonopore, since some groups have no penis proper). Many of the names that COOK gave to higher groups, and which refer to the penis (see HOFFMAN, 1980: 44) survive in the current classification of millipedes (HOFFMAN, 1980): Merocheta, Diplocheta, etc.

The julid penis is double in nature: there are two gonopores and the *vasa deferentia* remain separate throughout the length of the penis. The latter is therefore sometimes referred to as a double penis, or in the plural Latin form: penes. However, it is actually only its apical lobes which are paired, the penial basis being externally undivided. This is also true of several other julid families having a "double" penis, although in some the two "hemipenes" seem to be fully separated. The julid penis is devoid of setae, whereas penial setae occur in several other julidan families (Fig. 1). In most julids each apical lobe terminates in a hyaline "membranous tube" which probably may be retracted into the more basal, more sclerotized part of the apical lobe. The apical lobes are sometimes separated by a median lobe.

VERHOEFF (1926-32, p.687-689) described several important details of julid penis structure. His most important conclusions were:

1) The penis of *Pachyiulus* is fundamentally different from that of the other genera he examined: *Julus*, *Megaphyllum* (sub *Brachyiulus*), *Unciger* (sub *Oncoiulus*), *Ommatoiulus* (sub *Schizophyllum*), and *Leptoiulus*.

2) There may be considerable intraspecific variability, as demonstrated by *Unciger foetidus*.

3) Some genera seem to be characterized by particular penial features (*Ommatoiulus*: hood-like median lobe; *Leptoiulus*: penis slender, parallel-sided).

Several other authors have described the penis of various julid species but it was not until 1962 that another comprehensive treatment appeared, viz., in STRASSER's monograph of the erstwhile tribe Typhloiulini in which he presented outline drawings of the penis of 16 "typhloiuline" species (Fig. 32).

On this background, the aim of the present study is to explore the diversity of penis structure within the Julidae, and to assess the utility of the penis as a phylogenetic character by interpreting the differences found in a cladistic framework.

MATERIAL AND METHODS

More than a hundred species, representing fourty-four julid genera were examined, as well as representatives of all other julidan families (see appendix). Euparal mounts were made of isolated penes of many species, but some species were examined with the stereo microscope only. Some penes were prepared for scanning electron microscopy (SEM) through dehydration in absolute alcohol, transfer to acetone, and air-drying. After being mounted and coated with gold, the penes were examined with a Jeol SP840 scanning electron microscope. Drawing conventions: Although the paired gonoducts can often be seen by transparency, they have only been drawn in a few species.

INTRASPECIFIC VARIABILITY

VERHOEFF (1913) described intraspecific variability in penis shape, and named four varieties of *Unciger foetidus*, partly based on penial characters. The varieties appeared, at least in part, to be allopatrically distributed. Also STRASSER (1962), studying the Typhloiulini,

Source : MNHN, Paris

emphasized the individual variability. ENGHOFF (1995) found that in spite of modest individual variability, penis shape may be species-characteristic in the Paectophyllini and Calyptophyllini.

The present, more sweeping study suggests that at most moderate intraspecific variability is in fact the rule, and that penis characters therefore may be of taxonomic-phylogenetic value in the Julidae.

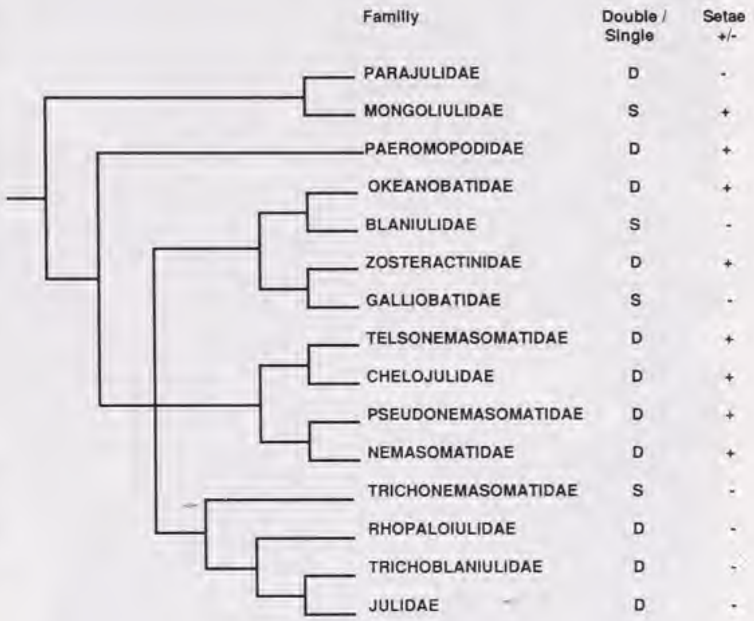


FIG. 1. — Penis types in julidan families. The cladogram is that of ENGHOFF (1991). The columns to the right show whether the penis is double (D) or single (S), and whether penial setae are present (+) or absent (-).

THE PENIS IN EACH JULID TRIBE

The tribes recognized by READ (1990) have been used as the taxonomic framework of this study, with a few modifications. The differences from READ (1990) are:

- Pteridoiulini are treated separately
- Catamicrophyllini and Symphyoiulini are included in Paectophyllini
- Calyptophyllini are considered
- Typhloiulini and Leptoiulini are included in Julini.

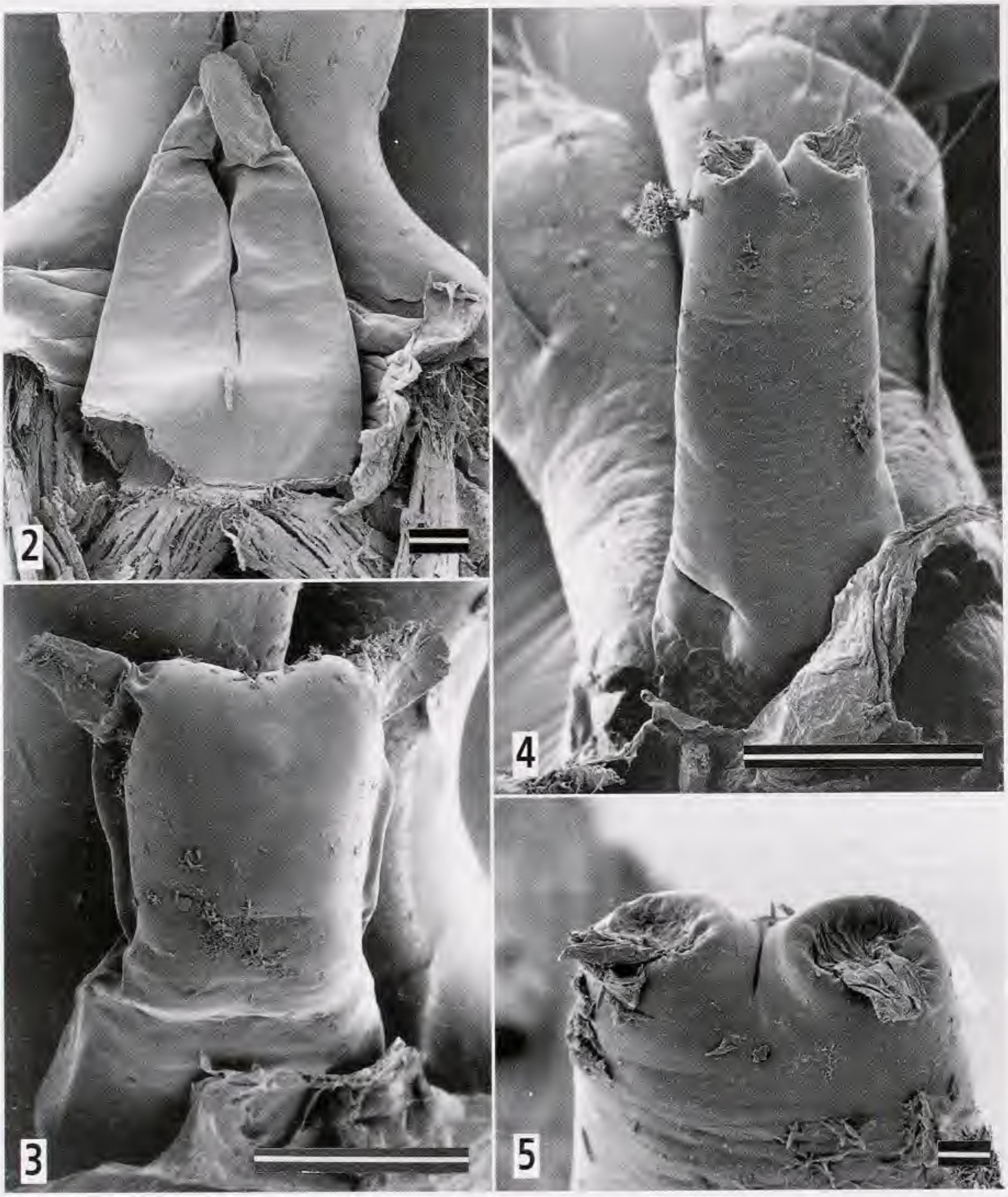
Neither this arrangement, nor the sequence of the tribes in the treatment reflects any definitive ideas about julid interrelationships. See, however, the section "Phylogenetic interpretation".

Pachyiulini

According to VERHOEFF (1926-32), the penis of *Pachyiulus* differs from that of the other julids in having the apical, separate lobes relatively much longer and lying parallel to each other (see Fig. 2). In the other julids, the separate apical lobes were much shorter and directed obliquely lateral.

Whereas the penis structure of "other julids" is much more diverse than envisaged by VERHOEFF, there is a remarkable constancy within the tribe Pachyiulini. ENGHOFF (1992) found that the penis in *Dolichoiulus* spp. is similar to that of *Pachyiulus*, and subsequent studies have shown this to be true of numerous genera of the tribe. All Pachyiulini have a hyaline penis, without any visible cuticular reinforcements. The two "hemipenes" are fused basally as in all julids, and the apical lobes are long and are lying parallel to each other (Figs 2, 6, 7). Only in *Mesoiulus ciliciensis* do the apical lobes diverge (STRASSER, 1975, confirmed by present study). There are no differentiated membranous tubes at the orifices, and there is no median lobe.

Source : MNHN, Paris

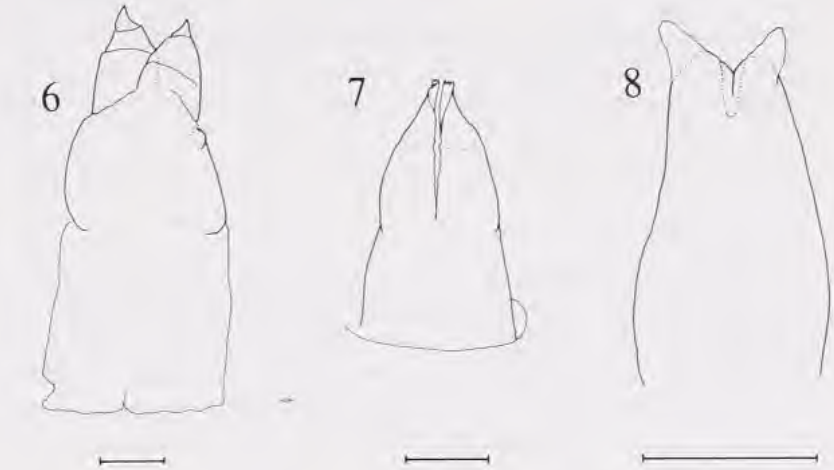


FIGS 2-5. — Scanning electron micrographs of penis in situ of 2: *Pachyiulus flavipes*, posterior view, 3: *Cylindroiulus caeruleocinctus*, posterior view, 4: *Ophyiulus pilosus*, posterior view, 5: *Ophyiulus pilosus*, close-up of tip, antero-distal view. Part of the second coxae is also shown in 2-4. - Scales: 0.1 mm (2-4), 0.01 mm (5).

Source : MNHN, Paris

Pteridoiulini

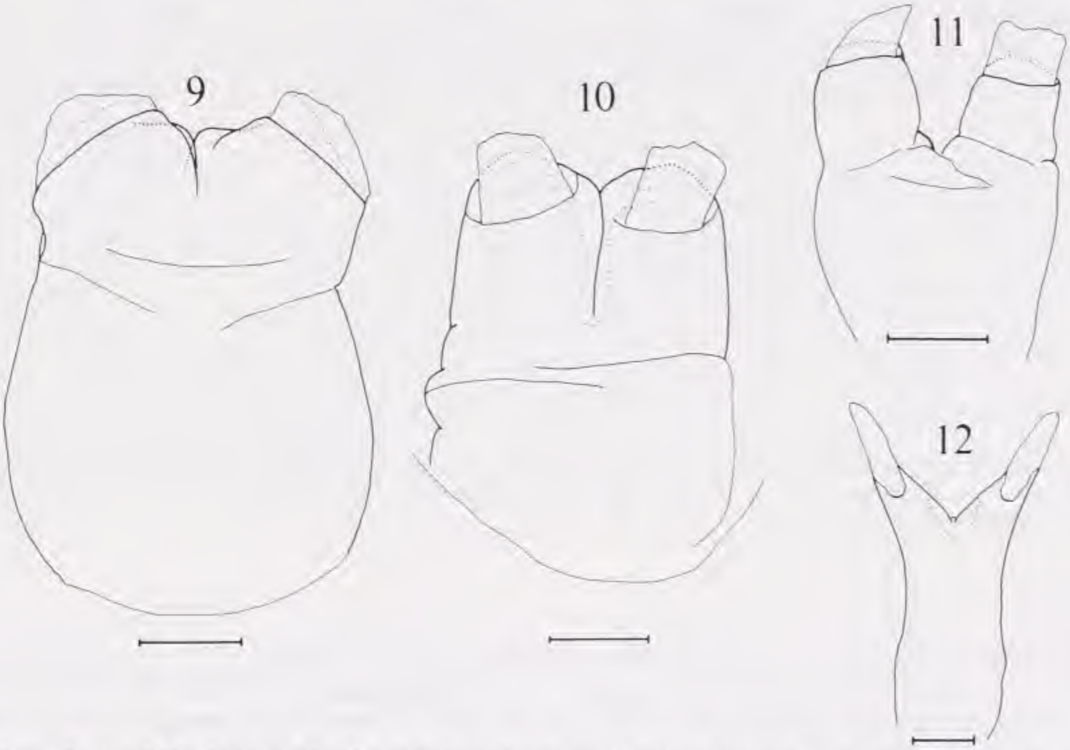
In *Pteridoiulus aspidiorum* (Fig. 8), the only species of this tribe, the body of the penis is somewhat less hyaline than in the pachyiulines. The apical lobes are short and each ends in a hyaline "membranous tube". The sclerotization of the penis is most evident in the narrow sinus between the apical lobes. There is no median lobe.



FIGS 6-8. — Penis of Pachyiulini (6, 7) and Pteridoiulini (8). 6: *Dolichoiulus vosseleri*, 7: *Amblyiulus barroisi*, 8: *Pteridoiulus aspidiorum*. - Scales: 0.1 mm.

Brachyiulini

In the genus *Brachyiulus* and in the genus *Megaphyllum*, the penis is very short and stout.



FIGS 9-12. — Penis of Brachyiulini. 9: *Megaphyllum hercules*, 10: *M. adanense*, 11: *Brachyiulus apfelbecki*, 12: *Anaulaciulus inaequipes*. - Scales: 0.1 mm (9, 12), 0.05 mm (10, 11).

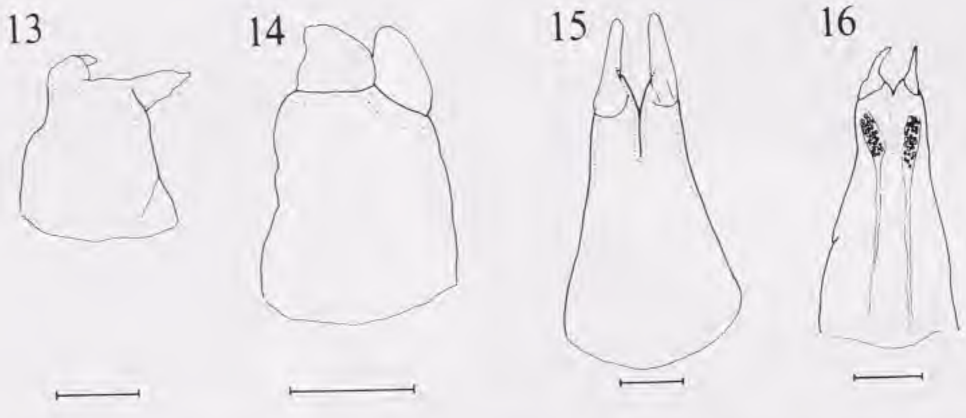
Source : MNHN, Paris

It is moderately sclerotized, and the lateral margins of the basal part only occasionally have a constriction (*M. hercules*, Fig. 9). The apical lobes are parallel and short (relatively long in *M. adanense*, Fig. 10); they lie close to each other in *Megaphyllum* (Figs 9 & 10) but are separated in *Brachyiulus apfelbecki* (Fig. 11). The membranous tubes are broad and ± parallel-sided. There is no median lobe. In *M. adanense* (Fig. 10), *M. geniculatum*, and *M. brachyurum* the membranous tubes do not arise apically but subapically on the caudal surface of the apical tubes - perhaps a synapomorphy for part of the large, catch-all genus *Megaphyllum*?

A deviating and characteristic penis type is found in the genus *Anaulaciulus*. Here the basal part of the well-sclerotized penis is slenderer and has concave lateral margins; the apical lobes are divergent and are drawn out into long, finger-shaped projections, giving a donkey-headlike outline to the penis (Fig. 12). KORSÓS (1996, this volume) found this penis type in numerous species of *Anaulaciulus* and suggested it to be an autapomorphy for the genus.

Leucogeorgiini

This small tribe shows great variability in penis structure. *Archileucogeorgia* (Fig. 13) and *Heteroiulus* (Fig. 14) have poorly sclerotized penes approaching the type found in Pachyiulini, although the apical lobes are shorter. *Chromatoiulus* (Fig.15) looks quite like the brachyiuline *Anaulaciulus*, although the long apical lobes are parallel rather than diverging. *Nepalmatoiulus* (Fig. 16) is well-sclerotized like *Chromatoiulus* but instead of being drawn-out the short apical lobes have long, slender well-differentiated membranous tubes. Neither genus has a median lobe.

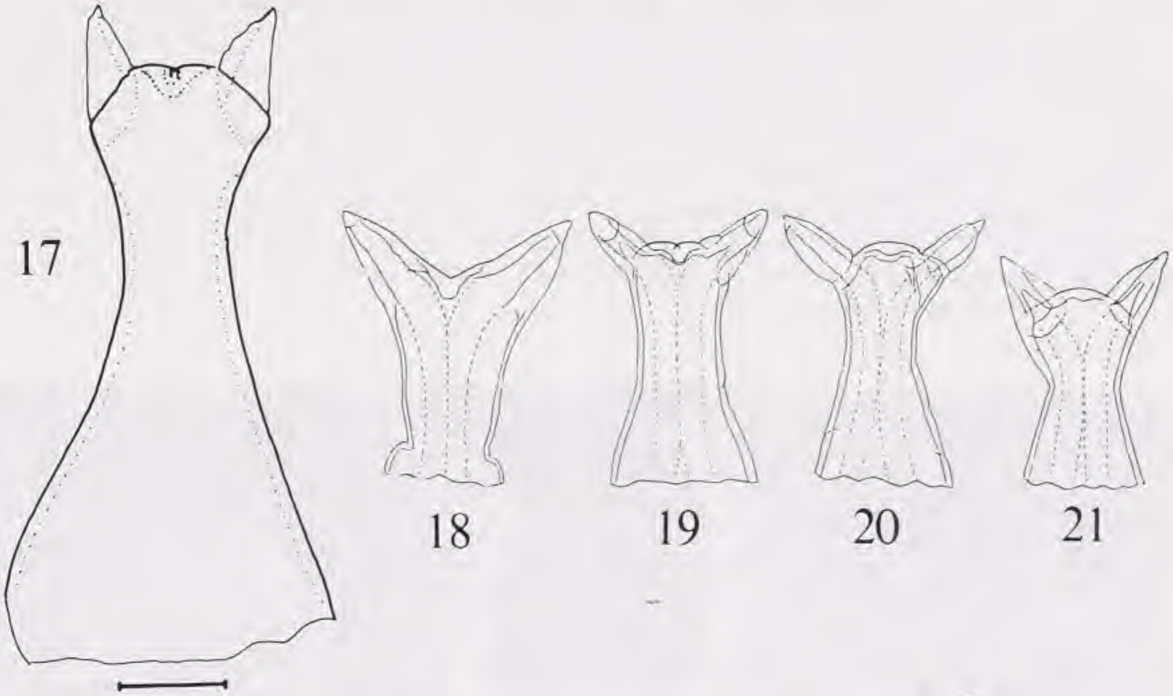


FIGS 13-16. — Penis of Leucogeorgiini. 13: *Archileucogeorgia* sp., 14: *Heteroiulus intermedius*, 15: *Chromatoiulus podabrus*, 16: *Nepalmatoiulus birmanicus* (with sperm ducts and spermatozoa shown). - Scales: 0.1 mm (13, 15, 16), 0.05 mm (14).

Oncoiulini

The penis of the only studied species, *Unciger foetidus* (Figs 17-21) looks quite like the penis found in most Cylindroiulini (see below): well-sclerotized, slender, with concave lateral margins, very short diverging apical lobes and well-differentiated membranous tubes. The species is notable for intraspecific variability, especially as regards the presence/absence and shape of a median lobe (VERHOEFF, 1913).

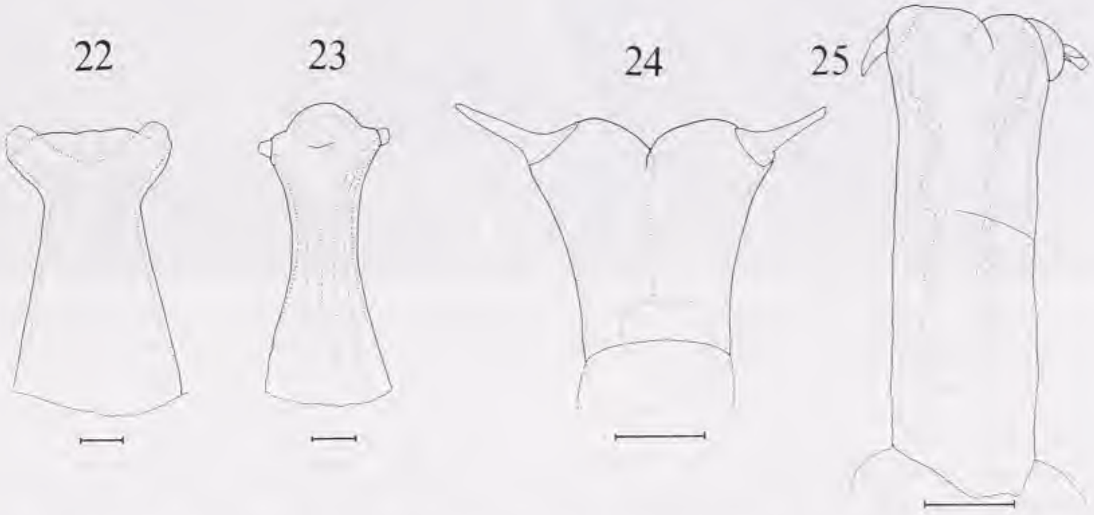
Source : MNHN, Paris



FIGS 17-21. — Penis of *Unciger foetidus* (Oncoiulini). 17: specimen from Italy, 18-21 (from VERHOEFF, 1913): specimens from Austria (18,19), Tatra Mts. (20), and Romania (21). - Scale (17): 0.1 mm.

Paectophyllini and Calyptophyllini

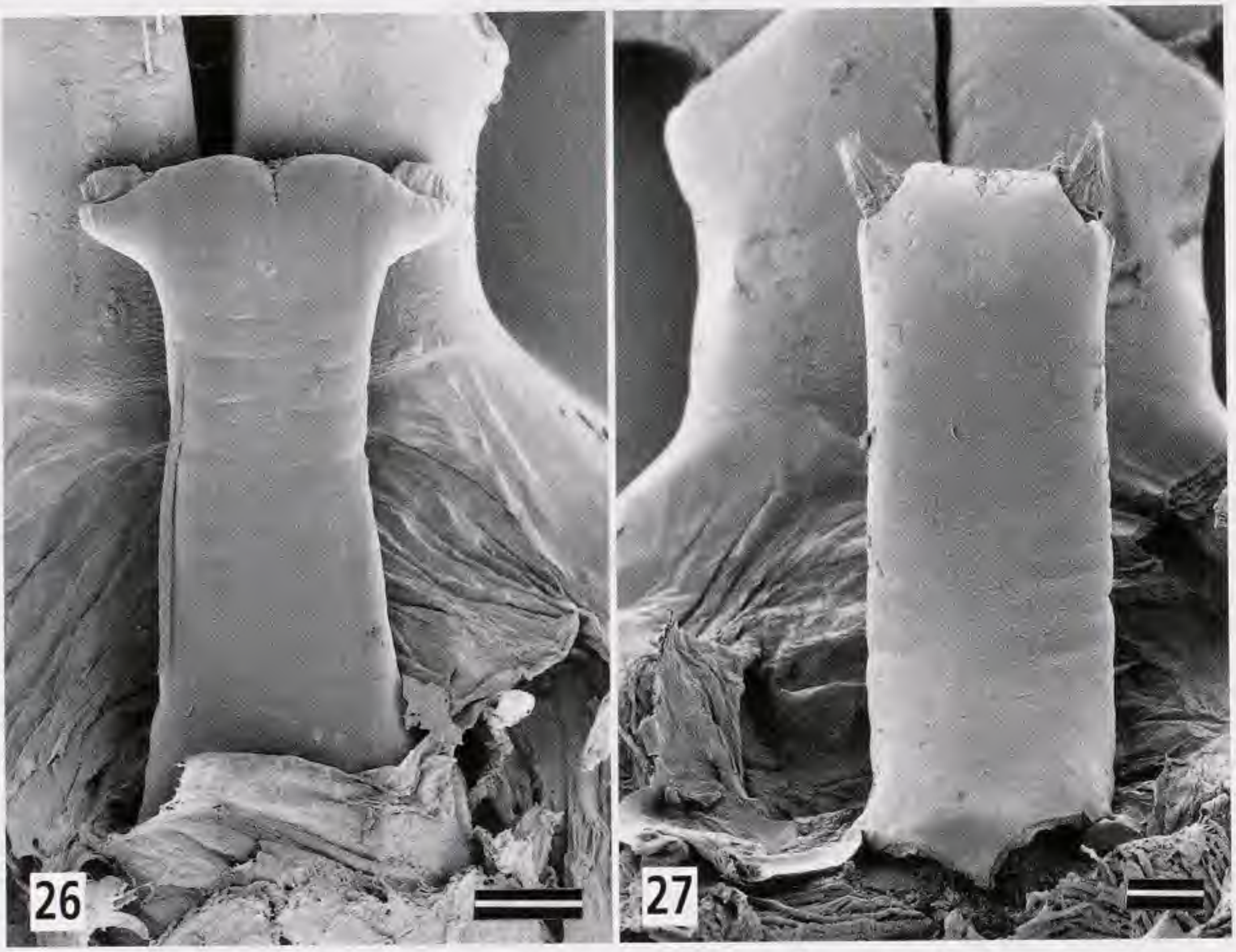
These two tribes, which are probably sister-groups (ENGHOFF, 1995) share a distinctive penis type characterized by relatively extreme sclerotization. The basal part may be either parallel-sided (Figs 25, 27), or with diverging (Fig. 24) or concave (Figs 22 - 23, 26) margins.



FIGS 22-25. — Penis of Paectophyllini (22, 23) and Calyptophyllini (24, 25). 22: *Macheiroiulus libicus*, 23: *Catamicrophyllum mesorientale*, 24: *Calyptophyllum trapezolepis*, 25: *C. digitatum*. Sperm ducts shown in 22, 23, and 25. - Scales: 0.1 mm.

Source : MNHN, Paris

The apical lobes are extremely short to apparently absent, with small membranous tubes. The apical margin may be straight (Fig. 27), emarginate (Figs 24-26, the emargination interpretable as representing the sinus between the apical lobes, or as representing a bipartite median lobe) or convex (Fig. 23, interpretable as representing an undivided median lobe). The detailed penis shape seems to be species-characteristic in several cases, although there is some individual variability. For instance, the penis of *Catamicrophyllum caifanum* may be parallel-sided as shown in Figure 27, or the lateral margins may diverge slightly; the apical margin may be simple as in Figure 27, or slightly concave. In *Macheiroiulus libicus*, the penis may have regularly converging lateral margins, or may be parallel except basally; the apical margin may be entire, or shallowly trilobate as in Figure 22.

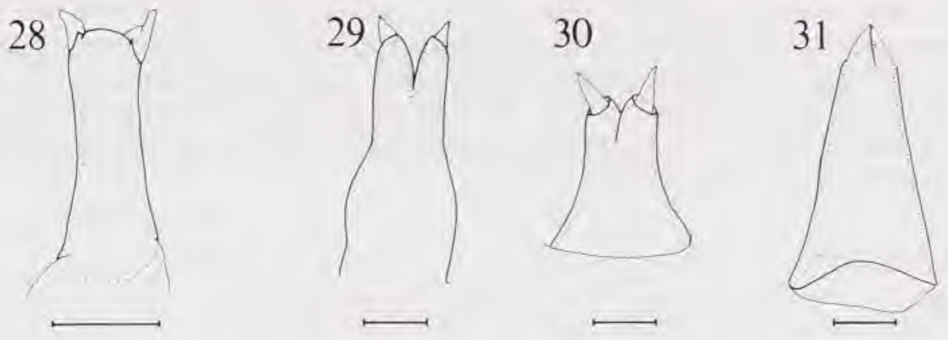


FIGS 26-27. — Scanning electron micrographs of penis in situ of Paectophyllini, posterior view. Part of the second coxae is also shown. 26: *Paectophyllum escherichii*, 27: *Catamicrophyllum caifanum*. - Scales: 0.1 mm.

Metaiulini

Metaiulus pratensis (Fig. 28), the only species of this tribe, has a penis which resembles that found in Paectophyllini and Calyptophyllini in being strongly sclerotized. Its shape also resembles that found in certain paectophyllines; in particular, the regularly convex apical margin, without any indication of a separation of two apical lobes, is a trait which is otherwise seen only in some *Catamicrophyllum* species (cf. Fig. 23).

Source : MNHN, Paris



FIGS 28-31. — Penis of Metaiulini (28) and Julini (29-31). 28: *Metaiulus pratensis*, 29: *Ophyiulus major*, 30: *Leptoiulus disparatus*, 31: *Julus scandinavius*. - Scales: 0.1 mm.

Julini

In the Julini the penis has well-differentiated apical lobes and membranous tubes. The apical lobes are usually very short (as in Fig. 4); those of *Ophyiulus major* (Fig. 29), are quite unusual for the tribe. In most species the penis is slender, although in a few, e.g., *Leptoiulus disparatus* (Fig. 30), it is stout. The lateral margins are often straight and parallel but may also be converging or concave. STRASSER (1962) studied the penis in several species of Typhloiulini (part of Julini in the present sense) and found that the penis shape was often characteristic of genera/subgenera in this group (see Fig. 32).

The genus *Julus* itself seems to be characterized by a very constant penis shape (Fig. 31). The lateral margins of the slender penis are straight and converging, and the short apical lobes and membranous tubes are closely applied to each other, so that the apical outline of the penis is distinctively angled. This shape was seen in all *Julus* species examined by me and was also recorded in *Julus terrestris* L., 1758, and *Julus scanicus* Lohmander, 1925 by LOHMANDER (1925). Of the other genera referred to Julini s.s. by HOFFMAN (1980) I have examined *Haplopodoiulus* where the penis is, however, similar to that found in *Ophyiulus* etc. On the other hand, the "typhloiulines" *Serboiulus lucifugus* and *Typhloiulus lobifer* appear to have penes like those in *Julus* (Fig 32, o, p).

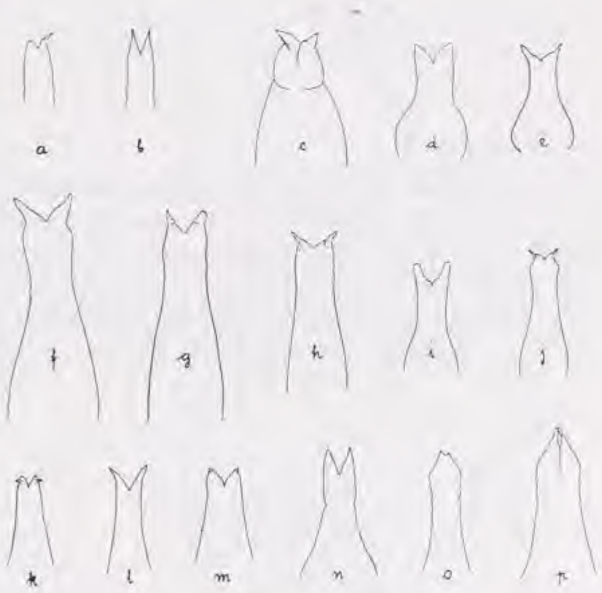


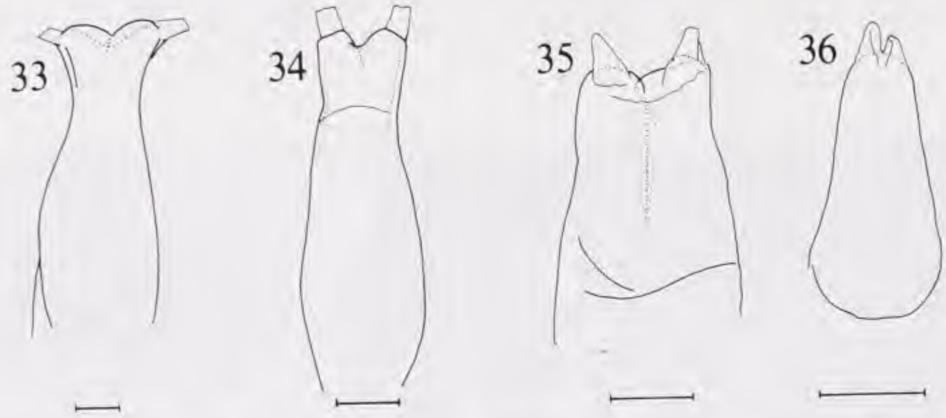
FIG. 32. — Penis of various "typhloiulines" (Julini) (from STRASSER, 1962). a: *Buchneria sicula* Strasser, 1959, b: *B. cornuta* Verhoeff, 1941, c: *Trogloiulus mirus* Manfredi, 1931, d: *T. boldorii* Manfredi, 1940, e: *Typhloiulus serbani* (Ceuca, 1956), f: *T. tobias* Berlese, 1886, g: *T. maximus* (Verhoeff, 1929), h: *T. ausugi* Manfredi, 1953, i: *T. illyricus* Verhoeff, 1929, j: *T. montellensis* Verhoeff, 1930, k: *T. albanicus* Attems, 1929, l: *T. bureschi* Verhoeff, 1926, m: *T. psilonotus* (Latzel, 1884), n: *T. strictus* (Latzel, 1882), o: *Serboiulus lucifugus* Strasser, 1962, p: *Typhloiulus lobifer* Attems, 1951.

Cylindroiulini

Most Cylindroiulini have a slender penis with very short apical lobes and well-

Source : MNHN, Paris

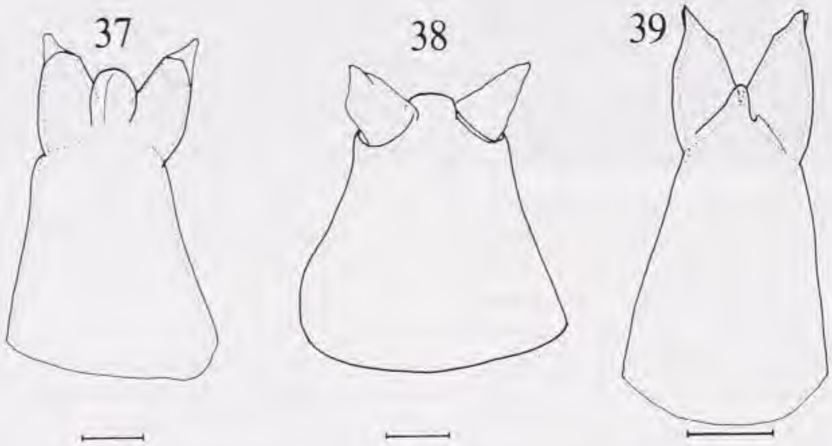
differentiated membranous tubes. The main difference from the Julini lies in the fact that the openings are separated by a distinct apical margin which is usually emarginate (Figs 3, 33, 34). *Cylindroiulus ruber* (Fig. 35) is somewhat deviating in being stouter. However, the penis of the closely related *C. bicolor* (cf. READ, 1992) looks like that found in most other cylindroiulines. *Styrioiulus pelidnus* (Fig. 36) deviates in having the lateral margins converging and the membranous tubes parallel close to each other.



FIGS 33-36. — Penis of Cylindroiulini. 33: *Cylindroiulus broti*, 34: *C. laurisilvae*, 35: *C. ruber*, 36: *Styrioiulus pelidnus*. - Scales: 0.1 mm.

Schizophyllini

Whereas the penis of *Tachypodoiulus* looks quite like that found in most Cylindroiulini, the examined species of *Ommatoiulus* differ in having a poorly sclerotized penis with a well-developed, undivided median lobe. In *O. rutilans* (Fig. 37) and *O. moreleti* the median lobe is remarkably well-developed: almost the same size as each of the well-differentiated apical lobes. In other species (Figs 38, 39) the median lobe is more modest. The apical lobes may be large and well-differentiated (Figs 37, 39) or virtually undifferentiated (Fig. 38).



FIGS 37-39. — Penis of Schizophyllini. 37: *Ommatoiulus rutilans*, 38: *O. kessleri*, 39: *O. navasi*. - Scales: 0.1 mm.

Source : MNHN, Paris

PHYLOGENETIC INTERPRETATION

In the light of the considerable variation in penis structure found both within the Julidae, and among julidan families, it appears worthwhile to examine whether penial characters may be useful for elucidating phylogenetic relationships. For the sake of clearness, the analysis is arranged in three hierarchical levels: family, tribe, and genus.

Family-level considerations

According to ENGHOFF (1981, 1991) the Julidae occupy a very subordinate phylogenetic position in the order Julida. The closest relatives of the family are, in descending order, three small families: Trichoblaniulidae, Rhopaloiulidae, and Trichonemasomatidae. Together with the Julidae, these families constitute the superfamily Juloidea, one of five superfamilies in the order.

The penis types found in the Julida can roughly be divided into four categories according to whether they are double (with separate gonopores) or single, and to whether they have setae or not (Fig 1). Using the Spirostreptida as an outgroup (the penis in the third juliformian order, Spirobolida, is highly deviant and hardly comparable), one may conclude that a double, setose penis is primitive within the Julida. All examined Spirostreptida have double penes, and although both setose and naked penes occur in this order, it is regarded more likely that the penial setae have been lost several times independently than that they have arisen several times independently. (Furthermore, the preliminary observations on Spirostreptida suggest that there may have been only one loss of penial setae). In the Julida at least four losses appear to have occurred (Fig. 1).

As shown in Figure 1 the Julidae agree with other Juloidea in lacking penial setae, and they agree with Trichoblaniulidae and Rhopaloiulidae in having a double penis. Lack of penial setae can be considered apomorphic for Juloidea but is a weak character since several non-Juloidea share the character. The double nature of the julid penis is obviously plesiomorphic.

The two closest relatives of Julidae, Trichoblaniulidae and Rhopaloiulidae agree in having the penis extremely short and without differentiation into membranous tube and basal part (Fig. 40). The longer penis of Julidae could therefore be interpreted as an autapomorphy of the family, but this interpretation is counterindicated by the generally longer penes found in Trichonemasomatidae and non-juloid Julida.

The penis therefore does not provide any very useful phylogenetic information at family-level.

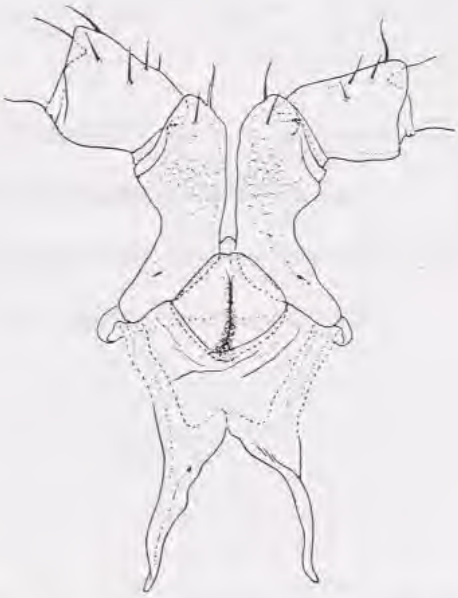


FIG. 40. — Penis in situ of *Trichoblaniulus hirsutus* (from BROLEMANN, 1923). The basal parts of the second legs are also shown, as are their tracheal apodemes.

Tribe-level considerations

In his classification of Diplopoda, HOFFMAN (1980) recognized three subfamilies of Julidae but admitted that "this family may merit the distinction of being the most difficult family of all diplopod groups to resolve". At the present state of knowledge of julid intra-family

Source : MNHN, Paris

phylogeny it therefore appears advisable to follow READ (1990) in only operating with one suprageneric categorial level: the tribe.

In the preliminary cladogram of julid tribes given by READ (1990) there is a basal trichotomy between Brachyiulini, Pachyiulini (incl. Pteridoiulini) and other julids. The "other julids" have a strong potential synapomorphy in the pro-mesomerital forceps of the gonopods, whereas neither of the two basal subfamilies have any convincing apomorphies.

The present study has confirmed the idea of VERHOEFF (1926-32): that the penis of Pachyiulini differs from that of other julids. Although the contrast is less striking than it appeared to VERHOEFF, the Pachyiulini are still distinguished by having a hyaline penis with relatively long, parallel apical lobes and no differentiated membranous tubes. Most other julids have the penis more or less sclerotized, the apical lobes are mostly shorter and are mostly directed obliquely lateral, and there are well-differentiated membranous tubes. Those non-pachyiulines which resemble the Pachyiulini in one or more penis characters are comfortably nested within groups with typical non-pachyiuline penis types. For instance, species of the genus *Ommatoiulus* have hyaline penes, and some species even have very long apical lobes. However, *Ommatoiulus* has convincing synapomorphies with *Tachypodoiulus*, the latter genus having a typical non-pachyiuline penis. *Ommatoiulus* + *Tachypodoiulus* (= Schizophyllini) in turn have synapomorphies with other non-pachyiulines (See READ, 1990: Fig. 16).

On the whole, the pachyiuline penis type more resembles that found in other julidan families, although the long apical lobes in Pachyiulini do not at all resemble the very short ones in Trichoblaniulidae and Rhopaloiulidae. In particular, the lack of differentiated membranous tubes is a trait shared with the non-julids.

The Pachyiulini might therefore tentatively be placed as sister-group to all other julids, which are united by the potential synapomorphy: "non-pachyiuline" penis, with differentiated membranous tubes. Pteridoiulini would have to be included with the latter group, the penis of *Pteridoiulus* being obviously non-pachyiuline (see Fig. 41).

A second tribe-level relationship supported by penial characters is the sister-group relationship between Paectophyllini (= Catamicrophyllini + Paectophyllini + Symphyoiulini in HOFFMAN, 1980 and READ, 1990) and Calyptophyllini. (ENGHOFF, 1995). Whether the resemblance between the penis type found in these tribes and in Metaiulini has any phylogenetic significance, remains to be shown.

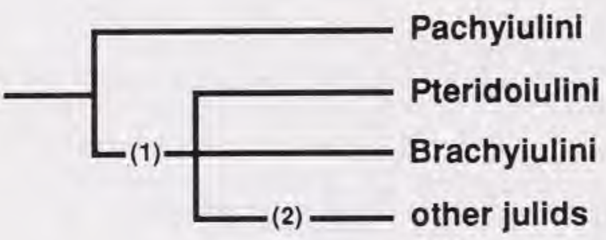


FIG. 41. — Tentative basal julid phylogeny. The non-pachyiulini penis type is a potential synapomorphy for non-pachyiuline julids (1). The gonopodal pro-mesomerital forceps is a potential synapomorphy for the "other julids" (2).

Genus-level considerations

Several julid genera have a consistent penis shape which in some cases may be regarded as a generic autapomorphy. This is probably true of

-*Anaulaciulus*, in which the apical lobes are diverging and are drawn out into long, finger-shaped projections (Fig. 12, see also KORSÓS, this volume).

-*Julus*, in which the lateral margins of the slender penis are straight and converging, and the short apical lobes and membranous tubes are closely applied to each other, so that the apical outline of the penis is distinctively angled (Fig. 31).

- perhaps some "Typhloiulini" (STRASSER, 1962).

Source : MNHN, Paris

-Ommatoiulus, in which the penis is poorly sclerotized and has a well-developed, undivided median lobe (Figs 37-39).

In some other cases, the potential significance of the penis lies at the subgeneric-species group level, as in some Typhloiulini (STRASSER, 1962) and in *Megaphyllum* (see above).

The penial similarity between *Tachypodoiulus* and *Cylindroiulus* deserves special mention, because this similarity would seem to support HOFFMAN's (1980) reallocation of *Tachypodoiulus* in the Cylindroiulini. It is, however, not clear whether the similarity is due to synapomorphy, symplesiomorphy or convergence, so the penial similarity cannot be regarded as a serious challenge to the similarities (in part clear synapomorphies) between *Tachypodoiulus* and *Ommatoiulus* mentioned by READ (1990).

CONCLUDING REMARKS

Although the phylogenetic conclusions of the present study may seem to be of modest extent, it is nonetheless obvious that future students of Julidae (and Juliformia in general) should pay more attention to penial characters than has been commonplace so far. A better understanding of the relationships between the numerous species of Julidae, many of which abound in a wide range of habitats in Europe, temperate Asia and (introduced) other temperate parts of the World, can only be achieved through consideration of all kinds of characters. Gonopods are good, but they are not everything.

ACKNOWLEDGEMENTS

I am grateful to the late Bent W. RASMUSSEN for help with scanning microscopy, to numerous colleagues for helping me to build up the large collection of julids in the Zoological Museum, Copenhagen, to J. GRUBER (Naturhistorisches Museum, Wien) for loan of *Rhopaloiulus*, and to Z. KORSÓS (Budapest) for access to his unpublished findings.

REFERENCES

BROLEMANN, H. W., 1923. — Biospeologica XLVIII. Blaniulidae, Myriapodes (Première Série). *Arch. Zool. exp. gén.*, **61** : 99-453, pl. i-xvi.

COOK, O. F., 1895. — Introductory note on the families of Diplopoda. [*In* : O. F. COOK & G. N. COLLINS, *The Craspedosomatidae of North America*.] *Ann. N.Y. Acad. Sci.*, **9** : 9-17.

ENGHOFF, H., 1981. — A cladistic analysis and classification of the millipede order Julida. *Z. zool. Syst. Evolut.-forsch.*, **19** : 285- 319.

ENGHOFF, H., 1987. — Revision of *Nepalmatoiulus* Mauriès 1983 - a southeast Asiatic genus of millipedes (Diplopoda: Julida: Julidae). *Courier Forsch.-Inst. Senckenberg* , **93** : 241-331.

ENGHOFF, H., 1991. — A revised cladistic analysis and classification of the millipede order Julida. With establishment of four new families and description of a new nemasomatoid genus from Japan. *Z. zool. Syst. Evolut.-forsch.*, **29** : 241-263.

ENGHOFF, H., 1992. — *Dolichoiulus* - a mostly Macaronesian multitude of millipedes. With the description of a related new genus from Tenerife, Canary Islands (Diplopoda, Julida, Julidae). *Ent. scand.*, **Suppl. 40** : 1-158.

ENGHOFF, H., 1995. — A revision of the Paectophyllini and Calyptophyllini: millipedes of the Middle East (Diplopoda, Julida, Julidae). *J. nat. Hist.*, **29** : 685-786.

HAACKER, U. & FUCHS, S., 1970. — Das Paarungsverhalten von *Cylindroiulus punctatus* Leach. *Z. Tierpsychol.*, **27** : 641-648.

HOFFMAN, R. L., 1980 [1979]. — *Classification of the Diplopoda*. Genève, Muséum d'Histoire naturelle, 237 pp.

HOFFMAN, R. L., 1961. — A new genus and subfamily of the diplopod family Nemasomatidae from the Pacific Northwest. *Proc. ent. Soc. Washington*, **63** : 58-64.

LOHMANDER, H., 1925. — Sveriges Diplopoder. *Göteborgs K. Vetensk.- o. Vitterh-Samh. Handl. 4 Följden*, **30** : 1-115.

READ, H., 1990. — The generic composition and relationships of the Cylindroiulini - a cladistic analysis (Diplopoda, Julida: Julidae). *Ent. scand.*, **21** : 97-112.

READ, H., 1992. — The genus *Cylindroiulus* Verhoeff 1894 in the faunas of the Caucasus, Turkey and Iran. *Senck. biol.*, **72** : 373-433.

Source : MNHN, Paris

SHELLEY, R. M., 1994. — Revision of the milliped family Paeromopodidae, and elevation of the Aprosphylosomatinae to family status (Julida: Paeromopodoidea). *Ent. scand.*, **25** : 169-214.

STRASSER, K., 1962. — Die Typhloiulini (Diplopoda Symphyognatha). - *Atti Mus. civ. Stor. nat. Trieste*, **23** : 1-77.

STRASSER, K., 1975. — Über einige Diplopoden aus der Türkei. - *Rev. suisse Zool.*, **82** : 585-597.

VERHOEFF, K. W., 1913. — Zur Kenntnis von *Haploporatia* und *Oncoiulus* (über Diplopoden 60. Aufsatz). - *Abh. naturw. Ges. ISIS Dresden* , **1** : 1-11.

VERHOEFF, K. W., 1926-1932. — Diplopoda 1 & 2. *In* : H. G. BRONNS *Klassen und Ordnungen des Tierreichs*, **5**, Leipzig, Akademische Verlagsgesellschaft : 1-2084.

APPENDIX: EXAMINED SPECIES

With the exception of *Rhopaloiulus cameratanus*, all examined material belongs to the Zoological Museum, University of Copenhagen.

NB : The Paeromopodidae sensu ENGHOFF (1981, 1991) have recently been divided into two families: Paeromopodidae and the monospecific Aprosphylosomatidae (SHELLEY, 1994) which together constitute the superfamily Paeromopodoidea. The penis of *Aprosphylosoma darceneae* Hoffman, 1961, is double and setose (HOFFMAN, 1961: Fig. 5), like that found in Paeromopodidae *sensu stricto*.

Class DIPLOPODA

FAMILY JULIDAE:

Pachyiulini
Amblyiulus barroisi (Porat, 1893)
"A." creticus (Verhoeff, 1901)
Baskoiulus stammeri Verhoeff, 1938
Chersoiulus sphinx Strasser, 1962
Dolichoiulus vosseleri (Verhoeff, 1900)
(+ 37 further spp. (see ENGHOFF 1992)
Japanoiulus lobatus Verhoeff, 1937
Mesoiulus ciliciensis Strasser, 1975
Pachyiulus flavipes (C. L. Koch, 1847)
Parapachyiulus recessus Golovatch, 1979
Rhodopiella beroni (Strasser, 1966)
Syrioiulus cf. *andreevi* Mauriès, 1984
S. continentalis (Attems, 1903)

Pteridoiulini
Pteridoiulus aspidiorum Verhoeff, 1913

Brachyiulini
Megaphyllum adanense (Verhoeff, 1943)
M. bosniense (Verhoeff, 1897)
M. brachyurum (Attems, 1899)
M. geniculatum (Lohmander, 1928)
M. hercules (Verhoeff, 1901)
M. rossicum (Timotheev, 1897)
M. taygeti (Strasser, 1976)
M. tenenbaumi (Jawlowski, 1931)
Brachyiulus apfelbecki Verhoeff, 1898
Anaulaciulus inaequipes Enghoff, 1986
A. tonginus (Karsch, 1881)

Leucogeorgiini
Heteroiulus intermedius (Brölemann, 1892)
Archileucogeorgia sp.
Chromatoiulus podabrus (Latzel, 1884)
Nepalmatoiulus birmanicus (Pocock, 1893)

Oncoiulini
Unciger foetidus (C. L. Koch, 1838)

Paectophyllini
Paectophyllum escherichii Verhoeff, 1898
Macheiroiulus compressicauda Verhoeff, 1901
M. libicus Manfredi, 1939
Symphyoiulus impartitus (Karsch, 1888)
Mesomeritius indivisus Enghoff, 1990
Catamicrophyllum caifanum Verh., 1901
C. mesorientale Enghoff, 1995

Calyptophyllini
Calyptophyllum digitatum Enghoff, 1995
C. trapezolepis Enghoff, 1995

Metaiulini
Metaiulus pratensis Blower & Rolfe, 1956

Julini s.l.
Julus scandinavius Latzel, 1884
J. colchicus Lohmander, 1936
J. subalpinus Lohmander, 1936
J. ghiljarovi Gulicka, 1963
J. jedryczkowskii Golovatch, 1981
Haplopodoiulus spathifer (Brolemann, 1897)
Pachypodoiulus eurypus (Attems, 1895)
Hypsoiulus alpivagus (Verhoeff, 1897)
Ophyiulus pilosus (Newport, 1843)
O. major Bigler, 1929
O. chilopogon (Berlese, 1886)
O. osellai Strasser, 1970
O. germanicus Verhoeff, 1896
O. targionii Silvestri, 1898
Leptoiulus broelemanni (Verhoeff, 1895)
L. cibdellus (Chamberlin, 1921)
L. macedonicus (Attems, 1927)
L. proximus (Nemec, 1896)
L. disparatus Lohmander, 1936
L. belgicus (Latzel, 1884)
L. alemannicus (Verhoeff, 1894)
L. tanymorphus (Attems, 1900)
Xestoiulus laeticollis (Porat, 1889)
Peltopodoiulus schestoperovi Lohmander, 1932
Chaetoleptophyllum sp.
Sibiriulus dentiger Gulicka, 1963
Pacifiiulus imbricatus Mikhaljova, 1982

Cylindroiulini
Allajulus spinosus (Ribaut, 1904)
Cylindroiulus broti (Humbert, 1893)
C. laurisilvae Enghoff, 1982
C. caeruleocinctus (Wood, 1864)
C. ruber (Lignau, 1903)
C. bicolor Lohmander, 1932
C. perforatus Verhoeff, 1905
C. latzeli (Berlese, 1884)
C. propinquus (Porat, 1870)
C. punctatus (Leach, 1815)
Styrioiulus pelidnus (Latzel, 1884)
Enantiulus dentigerus (Verhoeff, 1901)
Kryphioiulus occultus (C. L. Koch, 1847)

Schizophyllini
Tachypodoiulus niger (Leach, 1815)
Ommatoiulus cingulatus (Attems, 1927)
O. kessleri (Lohmander, 1927)
O. lapidarius (Lucas, 1846)
O. moreleti (Lucas, 1860)
O. navasi (Brolemann, 1919)
O. nivalis (Schubart, 1959)
O. oxypygus (Brandt, 1840)
O. rutilans (C. L. Koch, 1847)
O. sabulosus (L., 1758)

FAMILY TRICHOBLANIULIDAE
Trichoblaniulus hirsutus (Brölemann, 1889)

FAMILY RHOPALOIULIDAE
Rhopaloiulus cameratanus Attems, 1927

FAMILY TRICHONEMASOMATIDAE
Trichonemasoma peloponesius (Mauriès, 1966)

FAMILY NEMASOMATIDAE
Nemasoma varicorne (C. L. Koch, 1847)
Orinisobates spp.
Basoncopus filiformis Enghoff, 1985

FAMILY PSEUDONEMASOMATIDAE
Pseudonemasoma femorotuberculata Enghoff, 1991

FAMILY CHELOJULIDAE
Chelojulus sculpturatus Enghoff, 1982

FAMILY TELSONEMASOMATIDAE
Telsonemasoma microps Enghoff, 1979

FAMILY GALLIOBATIDAE
(*Galliobates gracilis* (Ribaut, 1909), see BROLEMANN 1923: Fig. 18)

FAMILY ZOSTERACTINIDAE
Ameractis chirogona Enghoff, 1982

FAMILY BLANIULIDAE
(see Brolemann 1923: Figs 39, 57)

FAMILY OKEANOBATIDAE
Okeanobates serratus Verhoeff, 1939
Yosidaiulus tuberculatus Takakuwa, 1940

FAMILY PAEROMOPODIDAE
Californiulus yosemitensis Chamberlin, 1941

FAMILY MONGOLIULIDAE
Skleroprotopus coreanus (Pocock, 1895)

FAMILY PARAJULIDAE
Aniulus sp.
Karteroiulus alaskanus (Cook, 1905)
Uroblaniulus sp.

Source : MNHN, Paris

Functional Morphology and Evolution of the Genitalia of Diplopoda - Helminthomorpha

Andreas TADLER

Institut für Zoologie, Althanstr. 14, A-1090 Wien, Austria

ABSTRACT

Theories about the evolution of genitalia (lock and key, genitalia recognition, pleiotropy, sensory female choice, mechanical mate choice) make different predictions about the mutual coadaptation between male and female genitalia. In three species of Chordeumatida and four species of Julida different degrees of mutual mechanical coadaptation between male and female genitalia have been found. This supports EBERHARD's "Mechanical Mate Choice Theory". The "Pleiotropy Hypothesis" cannot explain the evolution of diplopod genitalia because pleiotropic effects are prevented by heterochrony.

RÉSUMÉ

Morphologie fonctionnelle et évolution des genitalia des Diplopodes Helminthomorphes.

Les théories relatives à l'évolution des genitalia ("clé-serrure", reconnaissance des genitalia, pléiotropie, choix sensoriel des femelles, choix mécanique de l'accouplement), font appel à différentes hypothèses prédictives sur la coadaptation des genitalia mâles et femelles. Chez trois espèces de chordeumatides et quatre espèces de julides, différents degrés de coadaptation mécanique entre genitalia mâle et femelle ont été définis. Ceci vient tout d'abord appuyer la théorie de EBERHARD du "choix mécanique de l'accouplement". L'hypothèse "pléiotrope" ne peut pas expliquer l'évolution des genitalia de diplopode car les effets pléiotropiques sont évités par l'hétérochronie.

INTRODUCTION

In many animal groups, the genitalia show an evolutionary pattern quite different from other morpho-anatomic structures. The most important questions concern the "rapid and divergent evolution" (EBERHARD, 1985) and the high degree of complexity of genitalia.

The male gonopods in the Helminthomorpha serve as a good example for the phenomena of diversity and complexity. There were no really fundamental changes in the peripheral phenotype of Helminthomorpha since the middle of the paleozoic (KRAUS, 1974), however, the gonopods have developed completely different functional principles and "*Bauplans*" in each order and family (VERHOEFF, 1928-32).

Theories, which have been formulated to answer the general questions about the evolution of genitalia lead to predictions about morphological complexity of female genitalia and mutual mechanical coadaptation between male and female structures (see EBERHARD, 1985 for discussion).

TADLER, A., 1996. — Functional morphology and evolution of genitalia in Diplopoda - Helminthomorpha. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 327-330. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

The "lock and key" (DUFOUR, 1844, review: SHAPIRO & PORTER, 1989) and the "genitalic recognition" theories imply that sperm transfer between members of different species should be restricted. If a mechanical lock and key mechanism works, there should be a more or less tight mechanical fitting between male and female genitalia. In contrast, the genitalic recognition theory holds that heterospecific sperm transfer is avoided by species-specific stimulation. Therefore, the genitalia of females of different species should show differences in their sensory and nervous structures, but not in their morphology.

MAYR's "pleiotropy theory" (1963) proposes that genitalia are less subject to the corrective influences of natural selection and that changes in the structure of genitalia are caused by pleiotropic effects. The theory predicts that taxonomically important structural components of genitalia have no function. A tight mechanical correlation between male and female genitalia should not exist (KRAUS, 1968).

"Male competition" or "sperm competition" means that males can diminish the mating success of other males, for example, by displacing sperm from the receptacula of the female or by plugging the females' genitalia, so that the next male cannot deposit sperm (PARKER, 1970; SMITH, 1984). The theory predicts a rapid and divergent evolution of male genitalia, but no similar pattern in female genitalia.

The most recent theory is the "female choice theory " (EBERHARD, 1985). This theory supposes that females choose between males of their own species on the basis of genitalic structures. EBERHARD proposes two mechanisms, whereby female can discriminate between males:

1) Females discriminate between male genitalia on the basis of sensory structures, for example, mechanoreceptors. EBERHARD speaks about "internal courtship". Complexity of male genitalia arises because males evolve more and more efficient stimulatory organs. The theory predicts a rapid and divergent evolution of only male genitalia; female genitalia should be morphologically rather simple.

2) Females discriminate between male genitalia only by the mechanical fit. If genitalia mechanically fit well, then the probability of successful sperm transfer is high. This mechanical mate choice theory predicts that a morphological co-evolution between male and female organs occurs (EBERHARD, 1985).

GENITALIA FITTING IN DIPLOPODA

Analysis of diplopods frozen instantly during copulation shows that male gonopods do not represent simple casts of the female structures, but that there are different degrees of mutual mechanical coadaptation between male and female genitalia.

In *Nemasoma varicorne* (Julida, Nemasomatidae) the central area of the vulvae is modified to fit with the male solenomerit. In *Brachyiulus bagnalli* (Julida, Brachyiulidae), and *Cylindroiulus boleti* (Julidae, Cylindroiulinae) slits on the bursae of the female vulvae correspond to projections on the male gonopods. The female opercula of *Unciger foetidus* and *Cylindroiulus boleti* are modified to the different mechanical forces of the male pro-mesomerit forceps (HAACKER & FUCHS, 1970; TADLER, in press).

In three species of Chordeumatida different parts of the female vulvae are modified to fit with male parts.

On the vulvae of *Haploporatia eremita* (Mastigophorophyllidae), the margin bulge is enlarged. On the distal part of the anterior gonopods of the male, there are wing-like structures. In copula, the wing-like structures of the male gonopods fit between the margin bulge and the bursa of the female. In *Mastigona bosniense* (Mastigophorophyllidae), the basis of the vulvae is modified, so that during copulation the bursa can be rotated for more than 270 degrees. The sperm transferring distal part of the anterior gonopods is pressed by the basis against the openings of the receptacula (TADLER, 1989).

Source : MNHN, Paris

In *Craspedosoma transsilvanicum* (Craspedosomatidae) projections on the anterior gonopods of the male (terminal projection and clasping projection of the cheirite) insert into invaginations of the oviduct. During copulation the bursa of the female is pulled out from the vulval sac, the openings of the receptacula are thereby pressed against the sperm transferring parts of the male gonopods (brushes of the syncoxite) (TADLER, 1993).

DISCUSSION

The theories mentioned above are more or less mutually compatible. Genitalia could be influenced therefore by different evolutionary patterns.

According to the present observations, the most important factor for the evolution of genitalia of Helminthomorpha seems to be mechanical mate choice. Following MAYNARD SMITH (1987) female choice exists when some behaviour or structure of females causes them to mate more successfully with some males than with others. Therefore, even the simple evolutionary adaptation of male genitalia to female genitalia can be regarded as caused by female choice. It is important that the general theoretical models of female choice (FISHER, 1930; LANDE, 1981; BORGIA, 1987; POMIANKOWSKY, 1988) show that female choice concerns not only the evolution of male traits but also the evolution of female preferences. In our examples, change in female preference also means changes in female genital morphology. Therefore, the mechanical mate choice theory can explain the mutual mechanical adaptation of male and female genitalia (EBERHARD, 1985). Mechanical and sensory female choice may work together in Diplopoda, but unfortunately there is almost no information on the sensory structures of diplopod vulvae. Sensory female choice must therefore be examined by neuro-morphological and neuro-physiological studies.

The mechanical coadaptation between male and female genitalia may also be an indication that a lock and key mechanism works, but, of course the hypothesis must be tested, especially with regard to precopulatory isolation mechanisms.

A possible mechanism of sperm displacement has been found recently in a spirostreptid (BARNETT, TELFORD & DE VILLIERS, 1991), and there are even older observations, which suggest, that sperm competition exists in Diplopoda. For example the secretion caps (or "Kappenspermatophoren") described by VERHOEFF (1910) for the Chordeumatid *Mycogona germanica* may in fact be mating plugs. Sperm competition may be an important factor for the evolution of gonopods, however, it cannot explain the mechanical co-evolution between male and female genitalia.

PLEIOTROPY HYPOTHESIS

The existence of mutual mechanical coadaptation between male and female genitalia suggests that the pleiotropy hypothesis is less important.

For diplopods, one can turn the pleiotropy hypothesis around to arrive at a more plausible story. The two major groups of Diplopoda-Helminthomorpha, the Colobognatha and the Eugnatha, show great differences in the complexity and morphological diversity of gonopods. Whereas the gonopods of colobognaths are rather uniform and similar to walking legs, the gonopods of Eugnatha show a fantastic complexity and variety of forms (VERHOEFF, 1928-32). This may have to do with the ontogeny of the gonopods. Walking legs and gonopods are homologuous structures, but in Eugnatha, there is a heterochrony in the development of walking legs and gonopods. The legs of the seventh trunk unit of immature males either disappear entirely during post embryonic development or develop in to undifferentiated bumps (ENGHOFF, 1984).

It seems unlikely that in a metameric animal mutations would effect only a single segment. If there is no heterochrony, pleiotropic effects between gonopods and walking legs should be present. If, for example a mutation arises, which would have an advantageous effect for the

Source : MNHN, Paris

gonopods, perhaps because it makes an additional projection on the tarsus, the same mutation would be very disadvantageous for walking legs. The rapid and divergent evolution of complex gonopods in Eugnatha is perhaps made possible, since heterochrony prevents pleiotropic effects between the peripheral phenotype and the gonopods.

ACKNOWLEDGEMENT

I thank Peter ZULKA for many discussions and for converting the paper to a Macintosh Computer.

REFERENCES

BARNETT, M., TELFORD, S. R. & DE VILLIERS, C. J., 1991. — The genital morphology of the millipede *Orthoporus pyrhocephalus* (Diplopoda Spirostreptidae) - a possible mechanism of sperm displacement. *Proc. Electron Microscopy Soc. S. A.*, **21** : 15-17.

BORGIA, G., 1987. — A critical review of sexual selection models. *In* : J. W., BRADBURY & M. B., ANDERSON, *Sexual selection, testing the alternatives.* New York, Brisbane, Singapore, John Wiley & Sons, Chichester, 306 pp.

DUFOUR, L., 1844. — Anatomie générale des diptères. *Ann. Sci. nat.*, **1** : 244-264.

EBERHARD, W. G., 1985. — Sexual selection and animal genitalia. Cambridge Massachusetts, Harvard University Press, 244 pp.

ENGHOFF, H., 1984. — Phylogeny of millipedes, a cladistic analysis. *Z. zool . Syst u. Evolutionforsch.*, **22** : 8-26.

FISHER, R. A., 1930. — *The genetical theory of natural selection.* Oxford, Clarendon Press, 272 pp.

HAACKER, U. & FUCHS S., 1970. Das Paarungsverhalten von *Cylindroiulus punctatus* Leach. *Z. Tierpsych.*, **27** : 641-648.

KRAUS, O., 1968. — Isolationsmechanismen und Genitalstrukturen bei wirbellosen Tieren. *Zool. Anz.*, **171** : 22-38.

KRAUS, O., 1974. — On the morphology of Paleozoic diplopods. *Symp. Zool. Soc. London*, **32** :13-22.

LANDE, R., 1981. — Models of speciation by sexual selection on polygenetic traits. *Proc. natn. Acad. Sci. U.S.A.*, **78** : 3721-3725

MAYNARD SMITH, J., 1987. — Sexual selection - A classification of models. *In* : J. W. BRADBURY & M. B. ANDERSSON, *Sexual Selection: Testing the alternatives.* New York, Brisbane, Toronto, Singapore, John Wiley & Sons, Chichester.

MAYR, E., 1963. — *Animal species and evolution.* Cambridge, Massachusetts, Harvard University Press, 797 pp.

PARKER, G. A., 1970. — Sperm competition and its evolutionary consequences in insects. *Biol. Reviews* , **45** : 525-567.

POMIANKOWSKY, A. N., 1988. — The evolution of female mate preferences for male genetic quality. *Oxford. Surv. evol. Biol.*, **5** : 136-184.

SHAPIRO, A. M. & PORTER, A. H., 1989. — The lock and key hypothesis: evolutionary and biosystematic interpretion of insect genitalia. *Ann. Rev. Entomol.*, **34** : 231-245.

SMITH, R. L., 1984. — *Sperm competition and the evolution of animal mating systems.* Orlando, San Diego, New York, Academic Press, 687 pp.

TADLER, A., 1989. — Funktionsanatomie der Kopulationsorgane und Paarungsverhalten der Diplopoda-Chordeumatida *Craspedosoma transsilvanicum*, *Haploporatia eremita* und *Mastigona bosniense.* Dissertation, Univ. Wien, 100 pp.

TADLER, A., 1993. — Genitalia fitting, mating behaviour and possible hybridisation in millipedes of the genus *Craspedosoma* (Diplopoda, Chordeumatida, Craspedosomatidae). *Acta Zool. (Stockholm)* , **74** : 215-225.

TADLER, A., in press. — Functional morphology of genitalia of four species of julidan millipedes (Diplopoda, Nemasomatidae, Julidae). *Zool. J. Linn. Soc.*

VERHOEFF, K. W., 1910. — Juliden und Ascospermophora. *Jh. Ver. vaterl. Naturkde. Württemberg*, **66** : 337-398.

VERHOEFF, K. W., 1928-32. — Diplopoda. 2. *In* : H. G. BRONN's, *Klassen u. Ordnungen des Tierreichs.* Leipzig, Akademische Verlagsgesellschaft : 1073-2084.

Source : MNHN, Paris

Sperm Competition and the Evolution of Millipede Genitalia

Mandy BARNETT * & *Steven R.* TELFORD **

* Department of Zoology, University of Cape Town, Rondebosch 7700, South Africa
** Department of Zoology, University of Pretoria, Pretoria 0002, South Africa

ABSTRACT

Natural selection has presumably shaped much of genital morphology for the efficient transfer of sperm, but does not account for the evolution of seemingly bizarre male genitalic appendages. Gonopods of several species of spirostreptid millipedes were examined using light and scanning electron microscopy, and the sequence of events representative of their movement within the spermathecae demonstrated through the dissection of freeze-dried copula pairs and simulations using scale models. Gonopods bear devices that may function in sperm displacement, including flagellae with ridges and overlapping plates, scoops and regions of pitted spines. These are orientated correctly so as to facilitate sperm removal and are accomodated within the spermathecae of the females. This morphological evidence, coupled with spirostreptid physiology and behaviour, indicates that sperm competition may have played a major role in shaping gonopod morphology.

RÉSUMÉ

Transfert compétitif du sperme et évolution des genitalia des diplopodes.

La sélection naturelle a vraisemblablement beaucoup contribué à conformer la morphologie des genitalia pour un transfert efficace du sperme, mais elle n'explique pas l'évolution morphologique en apparence bizarre des appendices génitaux des mâles. Les gonopodes de plusieurs espèces de diplopodes spirostreptides ont été examinés en microscopie optique et en microscopie électronique à balayage et la séquence des évènements traduisant le mouvement des gonopodes à l'intérieur de la spermathèque a été mise en évidence par la dissection des pièces copulatrices et par des simulations à partir de modélisations. Les gonopodes portent des dispositifs variés qui interviennent dans le déplacement du sperme, incluant flagelles avec arêtes, lames se recouvrant, concavités et zones recouvertes d'épines enfoncées. Ils sont orientés de manière à faciliter la réception du sperme et s'accordent à la morphologie de la spermathèque des femelles. Cette évidence morphologique, couplée avec la physiologie et le comportement, indique que la compétition pour le transfert du sperme a pu jouer un rôle majeur dans la conformation morphologique du gonopode.

INTRODUCTION

Gonopods are taxonomic characters of primary importance in many millipedes (HOPKIN & READ, 1992) but, curiously, the selective processes responsible for the evolution of these complex structures have not been considered. Selection for effective sperm transfer presumably accounts for much of gonopod morphology, but, as in many taxa with complex genitalia (EBERHARD, 1985), does not fully explain their dramatic diversity.

BARNETT, M. & TELFORD, S. R., 1996. — Sperm competition and the evolution of millipede genitalia. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 331-339. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

The most likely explanation for this genital complexity is sexual selection, conceived by DARWIN (1871). Sexual selection is believed to operate through intrasexual (usually male-male) combat and intersexual (usually female) choice. In the context of intraspecific competition, sexual selection is believed to favour devices and behaviours of males that would prevent interference from other males before and during copulation (THORNHILL & ALCOCK, 1983). A significant new dimension to sexual selection theory is the concept of competition between the ejaculates of two or more different males for the fertilisation of ova (PARKER, 1970). Sperm competition occurs between the time of insemination and fertilisation. Mechanisms of sperm competition include the stratification, removal and dilution of ejaculates (BIRKHEAD & HUNTER, 1990). Because sperm competition is a powerful selective force in the evolution of reproductive behaviour and genital morphology (PARKER, 1970; SMITH, 1984; BIRKHEAD, 1989) it may simultaneously favour the evolution of devices that enhance an individuals ability to displace, replace or dilute a rival gametes, and behaviours that resist preemption of ejaculates (PARKER, 1970; WAAGE, 1984, 1986a; and see SMITH, 1984).

The behaviour and genital morphology of spirostreptid millipedes can be interpreted in the context of sperm competition. All the provisos for the evolution of sperm competition are fulfilled in millipede mating systems: they are polygynandrous, store sperm and fertilisation is delayed (TELFORD & DANGERFIELD, 1993a,b, c). Males protect their reproductive investment in females by prolonging the duration of copulation; a behaviour that is best interpreted as a form of mate guarding (TELFORD & DANGERFIELD, 1991, 1993c; BARNETT & TELFORD, 1994).

Here we focus on genitalic functional morphology and argue that gonopods are adaptive devices designed to displace (via stratification or removal) rival ejaculates. In support of this hypothesis, we present evidence to demonstrate that the gonopods reach the distal ends of the spermathecae, bear the necessary devices with which to displace sperm and, in some species, move within the spermathecae to effect sperm displacement.

MILLIPEDE GONOPODS

Millipede gonopods comprise three components; the sternite, the coxite and the telopodite, the latter of which contains the sperm canal. The gonopods are normally drawn into the body of the male so that only the distal ends of the coxites are visable. During copulation they are protruded and sperm are transferred from the penes to the coxite from where they are released into and stored in the spermathecae of the vulvae of the female (BARNES, 1986; KRABBE, 1982; BLOWER, 1985).

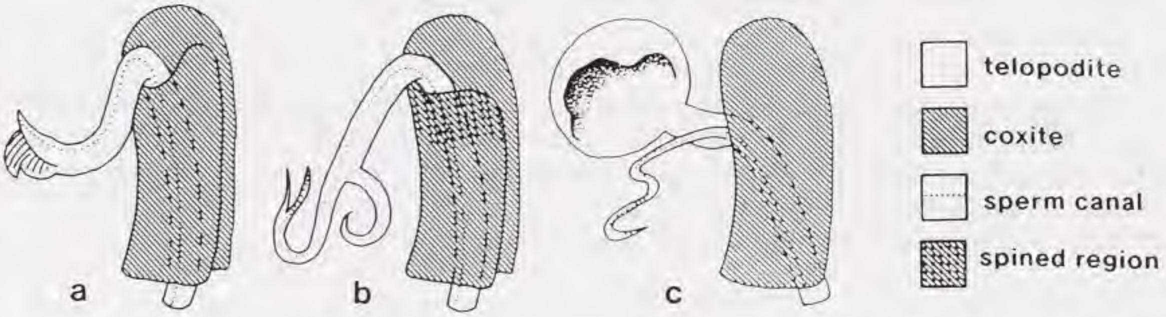


FIG. 1. — General plan of the LHS gonopod of (a) Harpagophoridae, (b) Spirostreptidae and the RHS gonopod of (c) Odontopygidae.

Source : MNHN, Paris

During copulation, the telopodite is retracted and released, causing it to perform a sequence of twists and turns that depend on the configuration of the telopodite arm and its association with the coxite. The general association of these components is family specific (Fig. 1).

In the Harpagophoridae and the Spirostreptidae, the telopodite is held within the gonocoel, a fold formed by the coxite. It originates at the base of the gonocoel and rises to its opening where it bends outwards, traversing the top of the lateral margin of the coxite. In the Harpagophoridae the telopodite typically ends in a rigid comb-like structure (ATTEMS, 1928, 1937). In the Spirostreptidae the telopodite varies from a single arm to one which bifurcates medially (ATTEMS, 1928, 1937). In addition, the Spirostreptidae typically bear a region of spines on the distal oral coxite (ATTEMS, 1928, 1937). These vary in form from stout to hair-like spines that may or may not be situated in pits.

The Odontopygidae have dramatically different gonopods. The telopodite originates at the base of the coxite but, because the coxite has no gonocoel, is not held within it. Instead it passes behind the coxite and bends inwards. Telopodites are proportionally larger than those of the Harpagophoridae and the Spirostreptidae and also bifurcate. The sperm canal is held within the whip-like arm.

GONOPODS AS DISPLACEMENT DEVICES

In order to actuate displacement, the gonopods need to bear morphological devices with which to manipulate rival sperm. In species shown to displace sperm (MC VEY & SMITTLE, 1984; SIVA-JOTHY, 1984, 1987; WAAGE, 1986a, b; MICHIELS & DHONT, 1988; RUBENSTEIN, 1989; MILLER, 1991; VON HELVERSON &

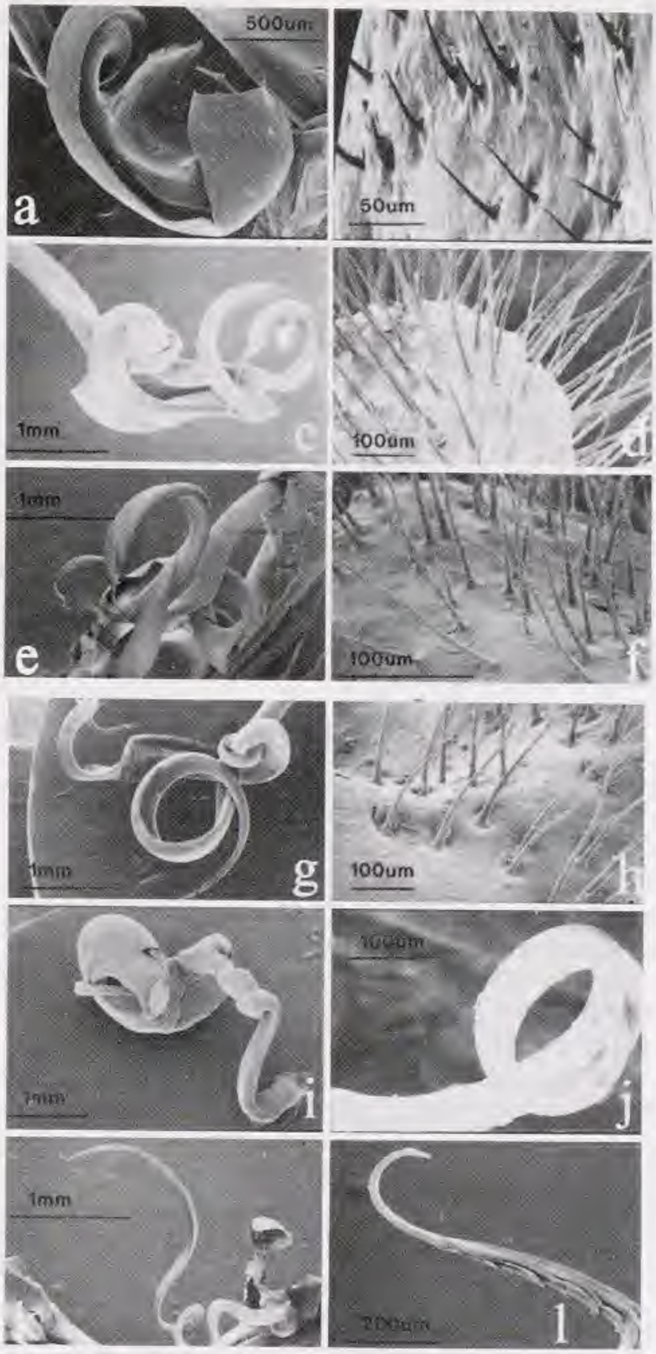


FIG. 2. — Scanning electron micrographs of gonopod features. *Orthoporus pyrocephalus* distal telopodite scoop (a) and region of spines (b); *Alloporus* sp. telopodite end (c) and spines (d); *Alloporus uncinatus* telopodite end showing medial scoop (e) and spines (f); *Doratogonus* sp. telopodite end (g) and spines (h); *Chaleponcus* sp. telopodite scoop (i) and distal end of sperm-canal bearing arm (j); *Chaleponcus limbatus* sperm-canal bearing arm (k) and overlapping plates at its distal end (l).

Source : MNHN, Paris

VON HELVERSON, 1991; GAGE, 1992) the morphological devices that have evolved to facilitate displacement include scoops (WAAGE, 1982), spines (WAAGE, 1986a, b) and flagellae with overlapping barbs (WAAGE, 1984).

Scoop-like structures occur on the telopodites of several species of millipede belonging to the families Odontopygidae and Spirostreptidae. These vary in form and in their position on the telopodite. In *Orthoporoides pyrocephalus,* L. Koch the telopodite terminates in a spade-like structure (Fig.2a). In *Chaleponcus* sp. the telopodite bifurcates, and one arm (the one not bearing the sperm canal) ends in a large rounded scoop (Fig. 2i). In addition, the sperm-canal bearing arm of the telopodite bears a series of ridges at its distal end (Fig. 2j). The telopodite of *Chaleponcus limbatus* also bifurcates with the sperm canal arm bearing a series of backwardly overlapping plates (Fig. 2k, l), and the other arm terminating in a less rounded scoop-like structure.

In *Alloporus* spp. and *Doratogonus* sp., where the telopodite also bifurcates, a trowel-like scoop occurs half way up the sperm canal bearing arm (Fig. 2c, e, g). The telopodites of species belonging to the family Harpagophoridae are more robust and terminate in rigid comb-like structures.

Interestingly, spines are found in some species belonging to the family Spirostreptidae but not in the other two families of Spirostreptid millipedes. The distal end of the oral region of the coxite is the only place on the gonopod where spines occur. These spines vary in form from stout pitted spines to long hair-like spines that are pitted in some species (Fig. 2b, h) and not in others (Fig. 2d, f).

COMPATIBILITY OF GONOPOD SIZE AND SPERMATHECAL SHAPE

To manipulate the sperm of rivals, a male's genitalia need to be able to access the areas of the female in which sperm are stored (PARKER, 1970; WALKER, 1980; KNOWLTEN & GREENWELL, 1984; WAAGE, 1986a). In insects, spermathecae range from relatively simple structures to complex convoluted organs, the latter of which may restrict access of the male genitalia to the site of sperm storage (EBERHARD, 1985). If sperm competition occurs via displacement, then spermathecal shape and size show strong correspondence (e.g damselflies: WAAGE, 1984, 1986a; dragonflies: WAAGE, 1986a; MILLER, 1991; and see WALKER, 1980; EBERHARD, 1985) to the size and shape of male genitalia (WAAGE, 1984, 1986a). This may prove to be a generalisation that holds true for all invertebrates that displace sperm.

In millipedes, female gonopores open into paired vulvae (BLOWER, 1985; HOPKIN & READ, 1992). These are opaque structures containing roughly oval chitinous structures which form the inner chambers of the spermathecae. The spermathecae open distally into oviducts that join to form a common oviduct running posteriorly to the ovaries (BARNETT, TELFORD & DE VILLIERS, 1993). Millipede spermathecae are relatively simple structures that are species specific in both shape and size (Fig. 3).

To actuate effective manipulation (and placement) of sperm, selection should favour the evolution of structures that can reach the areas of the spermathecae where the sperm are stored. In millipedes the chitinous inner chamber of the spermatheca appears to be the main site of sperm storage (unpublished data). For each species examined, the distal ends of the telopodites of males can be accomodated within the spermathecae and can easily reach their distal ends. Thus, the manipulation of sperm held within these regions of the female reproductive tract is possible.

Female sperm storage organs can be very complex structures with highly sophisticated muscular control (e.g. VILLAVASCO, 1975). Thus, females may be able to exert some control over fertilisation events resulting in selection acting on males to overcome this control. This conflict of interest can generate an escalating evolutionary spiral, or arms race (*sensu* DAWKINS & KREBS, 1979) between the sexes to gain control over copulatory events. The outcome of this process of co-evolution would be concomitant genitalic adaptation and perhaps structural complexity. The latter is true for millipede gonopods but not spermathecae.

Source : MNHN, Paris

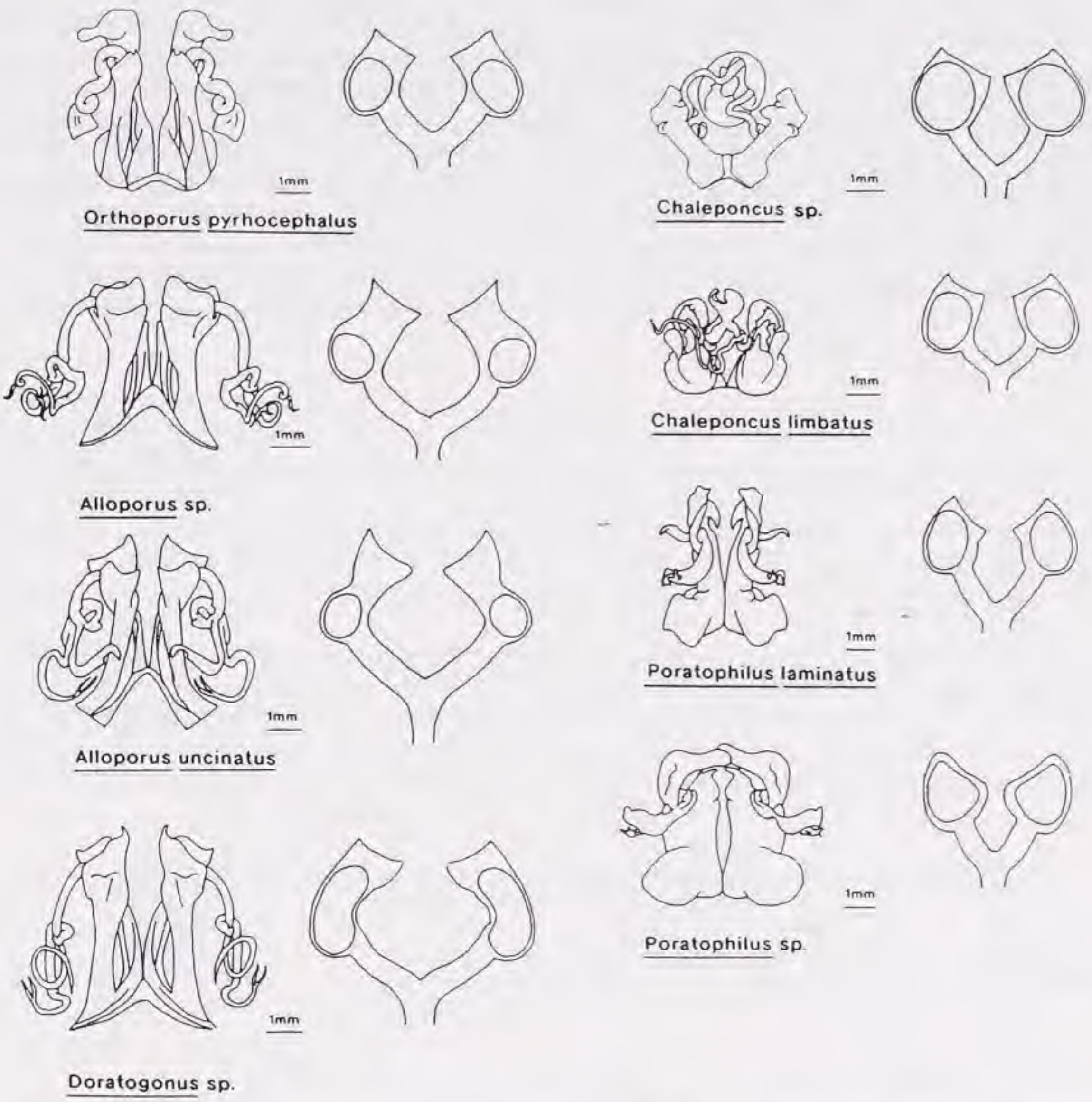


FIG. 3. — Diagrammatic representations of corresponding gonopods and spermathecae. The oval shapes within the spermathecae represent the chitinous inner chambers. (*Orthoporus* = *Orthoporoides* in the text; *Poratophilus* = *Zinophora* in the text)

Interestingly, the size of the genitalia is not related to the body sizes of the animals. *Chaleponcus* sp. is one of the smallest species (mean mass(g) = 2.49, SD = 0.4, n = 45) and its spermathecae are as large as those of *Alloporus uncinatus* (mean mass(g) = 9.31, SD = 5.99, n = 295). Spermathecal size and shape in *Chaleponcus* sp. corresponds precisely with the large scooped distal ends of the telopodites of the gonopods of conspecific males. It should also be noted that present descriptions of spermathecal shape are based on external topography; internal shape may be different. Also, gonopods and/or female musculature may expand and alter the shape of spermathecae during copulation (see VILLAVASCO, 1975; SIVA-JOTHY, 1987; WALKER, 1980; MILLER, 1987, 1991).

Source : MNHN, Paris

GONOPOD ORIENTATION AND MOVEMENT WITHIN THE SPERMATHECAE

Movement of the gonopods is effected by retracting the proximal end of the telopodite and is determined by both the point of emergence of the telopodite from the coxite and the shape of the telopodite arm. Retraction-release sequences have been reconstructed for two of the species examined here, and illustrate that describing the structure of the distal end of the telopodite is not sufficient to fully explain its functional morphology. The shape of the telopodite arm, and particularly the number and tightness of spirals that it describes are critical in determining its movement path within the spermatheca and hence its sperm displacement action. For example, in *Orthopoides pyrocephalus*, the telopodite emerges at the distal end of the coxite. When it is retracted, it traverses the bridge formed by the margin at the fold of the coxite. The scoop at its distal end twists within the spermathecae and is then brushed against the spined region on the distal coxite. This movement may be a mechanism whereby sperm could be removed from the spermatheca prior to insemination (Fig. 4).

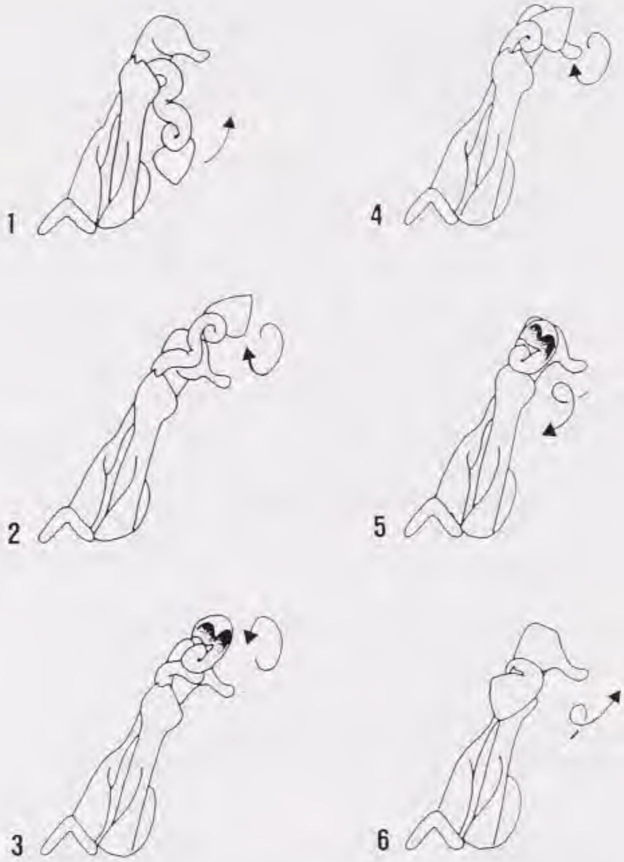


FIG. 4. — Telopodite retraction-release cycle for the RHS gonopod of *Orthoporoides pyrocephalus*. Proximal retraction of the gonopod causes the distal end to rise (2); twist forward (3); twist back (4); twist forward (5) and then flip round to make contact with the spined region of the coxite. Release of the telopodite results in the scoop brushing downwards against the spines. Source: Modified from BARNETT, TELFORD & DE VILLIERS 1993.

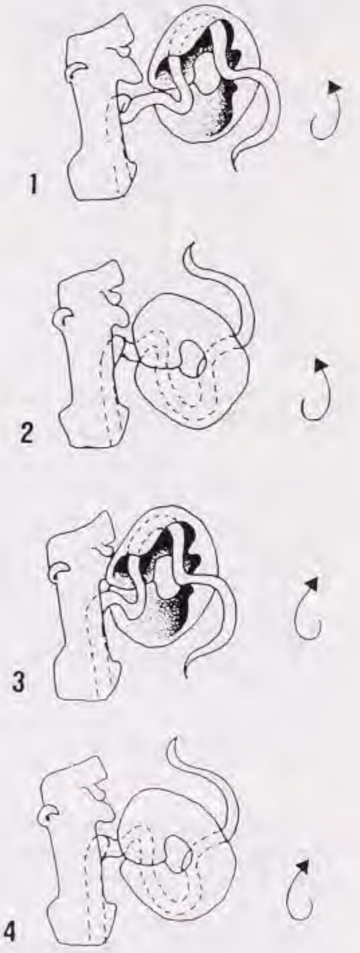


FIG. 5. — Telopodite retraction-release cycle of *Chaleponcus* sp. Retraction causes the scoop to twist about its own axis, flipping forward (2); forward again (3); then backwards (4) and backwards again (1).

Source : MNHN, Paris

In contrast, the telopodite of *Chaleponcus* sp. emerges from the posterior base of the coxite and retraction yields a rotation of the scoop about its own axis. There are no spines against which the scoop is brushed, and it is predicted that the scoop functions to reposition or mix sperm within the spermathecae but not to remove it (Fig. 5).

This comparison serves to illustrate how two apparently similar structures can have different functions due to the shape of the telopodite arm and its resultant plane of movement. Thus, the evolution of sperm displacing devices in millipedes will not only be linked to the actual displacing structures, namely the distal ends of the telopodites, but to the gonopods as a whole because the mechanism of movement is dependent on the coxite, the shape of the telopodite arm, and associated structural modifications. This is in contrast to the damselflies in which simple horizontal movements during copulation make it possible to predict the mechanism of sperm competition from the morphology of the terminal region of the penis (WAAGE, 1984, 1986a).

CONCLUSIONS

The evolution of complex genital morphology in millipedes can be explained and understood in the context of sperm competition. Gonopods display the design features necessary for efficient sperm displacement and their complexity is probably a product of sexual selection via sperm competition. While sperm competition implies a focus on intermale competition, the evolutionary perpective of females is also critical to understanding genitalic evolution (KNOWLTON & GREENWELL, 1984). The spermathecae provide the arena for competitive interactions and females may be capable of dictating the outcome of the competition (WALKER, 1980; EBERHARD, 1985).

The relatively simple spermathecal structures of female millipedes contrast with male gonopod complexity. This suggests that the manipulative capabilities of the gonopods dictate the intensity of sperm competition and resultant patterns of sperm precedence.

Structural modifications of the terminal region of the telopodite and the shape of the telopodite arm together may provide an accurate prediction of gonopod functional morphology (see Table 1).

TABLE 1. — Between species comparisons of gonopod functional morphology, predicted mechanisms of sperm competition and sperm precedence patterns.

FAMILY	SPECIES	GONOPOD FEATURES TELOPODITE	COXITE	DISPLACEMENT MECHANISM	PRECEDENCE PATTERN
SPIROSTREPTIDAE					
	O. pyrocephalus	distal scoop	stout spines	removal	last male
	A. uncinatus	medial scoop	hair-like spines	stratification	last male
	Alloporus sp.	medial scoop	hair-like spines	stratification	last male
	Doratogonus sp.	medial scoop	hair-like spines	stratification	last male
ODONTOPYGIDAE					
	C. limbatus	distal scoop & flagellum	--	removal	last male
	Chaleponcus sp.	distal scoop & flagellum	--	stratification	first male
HARPAGOPHORIDAE					
	Z. laminata	distal comb	--	removal	last male
	Zinophora sp.	distal comb	--	removal	last male

Where displacement of rival ejaculates occurs then last-male sperm precedence is the expected outcome of a multiple mating sequence (see WAAGE, 1986a; MILLER, 1991). Our data

Source : MNHN, Paris

predict last-male precedence in all but one species (*Chaleponcus* sp., Table 1). We have shown that sperm mixing or first-male precedence is likely to occur in this species (unpublished data). This is because the scoop-like terminal region of the telopodite redistributes rather than removes rival ejaculates; a consequence of the shape of the telopodite arm. These results suggest a cautious approach to ascribing a precise function to a structure without a complete understanding of its mode of action.

Descriptive studies of genital morphology are an essential first step towards understanding the precise function of these complex structures. Knowledge of the mode of action of the gonopods allows *a priori* predictions to be made about mechanisms of sperm displacement and patterns of sperm precedence. This is an essential basis for beginning an iterative series of experiments and manipulations designed to quantify mechanisms of sperm competition in millipedes. Although numerous studies have quantified patterns of sperm precedence (see SMITH, 1984), few have attempted the more challenging task of unravelling the underlying mechanisms.

REFERENCES

ATTEMS, C., 1928. — The Myriapoda of South Africa. *Ann. S. A. Mus.*, **26** : 353-354.

ATTEMS, C., 1937. — The myriapoda of Natal and Zululand. *Natal Mus. Ann.*, **7** : 459-522.

BARNES, R. D., 1986. — *Invertebrate Zoology*. Philadelphia, Saunders College Publishing, 743 pp.

BARNETT, M., TELFORD, S. R. & DE VILLIERS, C. J., 1993. — Sperm displacement in a millipede? - an investigation into the genital morphology of the southern African Spirostreptid millipede *Orthoporus pyrhocephalus*. *J. Zool. Lond.*, **211** : 511-522.

BARNETT, M. & TELFORD, S. R., 1994. — The timing of insemination and its implications for sperm competition in a millipede with prolonged copulation. *Anim. Behav.*, **48** : 482-484.

BIRKHEAD, T. R., 1989. — The intelligent sperm? A concise review of sperm competition. *J. Zool. Lond.*, **218** : 347-351.

BIRKHEAD, T. R. & HUNTER, F. M., 1990. — Mechanisms of sperm competition. *Trends Ecol. Evol.*, **5** : 48-52.

BLOWER, J. G., 1985. — *Millipedes* (*Synopses of the Br. Fauna* NS, **35**). London, E. J. Brill & W. Backhuys, 242 pp.

DARWIN, C., 1871. — *The descent of man and selection in relation to sex*. London, John Murray, 693 pp.

DAWKINS, R. & KREBS, J. R., 1979. — Arms races between and within species. *Proc. R. Soc. Lond.*, **205** : 489-511.

EBERHARD, W. G., 1985. — *Sexual selection and animal genitalia*. Cambridge, Harvard, University Press, 231 pp.

GAGE, M. J. G., 1992. — Removal of rival sperm during copulation in a beetle, *Tenebrio molitor*. *Anim. Behav.*, **44** : 587-589.

HOPKIN, S. P. & READ, H. J., 1992. — *The biology of millipedes*. Oxford, Oxford Univ. Press, 233 pp.

KNOWLTEN, N. & GREENWELL, S. R., 1984. — Male sperm competition avoidance mechanisms: The influence of female interests. *In:* R. L. SMITH, *Sperm competition and the evolution of animal mating systems*. New-York, Academic Press : 62-83.

KRABBE, E., 1982. — Systematik der Spirostreptidae (Diplopoda: Spirostreptomorpha). *Abh. naturw. ver. Hamburg (N.F.)*, **24** : 1-146.

MCVEY, M. E. & SMITTLE, B. J., 1984. — Sperm precedence in the dragonfly *Erythemis simplicicollis*. *J. Insect Physiol.*, **30** : 619-628.

MICHIELS, N. K. & DHONT, A. A., 1988. — Direct and indirect estimates of sperm precedence and displacement in the dragonfly *Sympetrum danae*. *Behav. Ecol. Sociobiol.*, **23** : 257-263.

MILLER, P. L., 1987. — Sperm competition in *Ischnura elegans*. *Odonatologica* **16** : 201-207.

MILLER, P. L., 1991. — The structure and function of the genitalia in the Libellulidae (Odonata). *Zool. J. Linn. Soc.*, **102** : 43-73.

PARKER, G. A., 1970. — Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.*, **45** : 525-567.

RUBENSTEIN, D. I., 1989. — Sperm competition in the water strider *Gerris remigis*. *Anim. Behav.*, **38** : 631-636.

SIVA-JOTHY, M. T. 1984. — Sperm competition in the family Libellulidae (Anisoptera) with special reference to *Crocothemis erythraea* (Brulle) and *Orthetrum cancellatum* (L.). *Adv. Odonatol.*, **2** : 195-207.

SIVA-JOTHY, M. T. 1987. — The structure and function of the female sperm storage organs in libellulid dragonflies. *J. Insect Physiol.*, **33** : 559-567.

Source : MNHN, Paris

SMITH, R. L. 1984. — *Sperm competition and the evolution of animal mating systems.* New York, Academic Press, 687 pp.

TELFORD, S. R. & DANGERFIELD, J. M., 1991. — Sex ratio manipulation and copulation duration in the tropical millipede, *Alloporus uncinatus*: A test of the copulatory guarding hypothesis. *Anim. Behav.*, **40** : 984-986.

TELFORD, S. R. & DANGERFIELD, J. M., 1993a. — Mating tactics in the tropical millipede *Alloporus uncinatus* (Diplopoda; Spirostreptidae). *Behaviour*, **124** : 45-50.

TELFORD, S. R. & DANGERFIELD, J. M., 1993b. — Mating behaviour and mate choice experiments in some tropical millipedes (Diplopoda: Spirostreptidae). *S. A. J. Zool.*, **28** : 155-160.

TELFORD, S. R. & DANGERFIELD, J. M., 1994. — Males control the duration of copulation in the tropical millipede, *Alloporus uncinatus*. *S. A. J. Zool.*, **29** : 266-268.

THORNHILL, R. & ALCOCK, J., 1983. — *The evolution of insect mating systems.* Cambridge, Massachusetts, Harvard, University Press, 547 pp.

VILLAVASCO, E. J., 1975. — Functions of the spermathecal muscle of the boll weevil, *Anthonomus grandis*. *J. Insect. Physiol.*, **21** : 1275-1278.

VON HELVERSON, D. & VON HELVERSON, O., 1991. — Premating sperm removal in the bushcricket *Metaplastes ornatus*. *Behav. Ecol. Sociobiol.*, **28** : 391-396.

WAAGE, J. K., 1982. — Sperm displacement by male *Lestes vigilax* (Zygoptera: Lestidae). *Odonatologica*, **11** : 201-209.

WAAGE, J. K., 1984. — Sperm competition and the evolution of odonate mating systems. *In* : R. L. SMITH, *Sperm Competition and the Evolution of Animal Mating Systems.* New-York, Academic Press : 251-288.

WAAGE, J. K., 1986a. — Evidence for widespread sperm displacement ability among Zygoptera (Odonata) and the means for predicting its presence. *Biol. J. Linn. Soc.*, **28** : 285-300.

WAAGE, J. K., 1986b. — Sperm displacement by two libellulid dragonflies with disparate copulation durations. *Odonatologica*, **15** : 429-444.

WALKER, W. F., 1980. — Sperm utilisation strategies in nonsocial insects. *Am. Nat.*, **115** : 780-799.

Source : MNHN, Paris

Source : MNHN, Paris

Preliminary Data on the Anatomy of the Genital Systems in *Craterostigmus tasmanianus* (Craterostigmomorpha) and *Esastigmatobius longitarsis* (Henicopidae, Lithobiomorpha) (Chilopoda)

Carol C. PRUNESCU *, *Robert MESIBOV* **& *Keizaburo SHINOHARA* ***

* Institute of Biology, 296 Spl. Independentei, RO-79651 Bucarest, Romania
** P.O. Box 431, Smithton, Tasmania 7330, Australia
*** 7-4, Wakamiya, 2-chôme, Ichiara-si, J-Chiba 290, Japan

ABSTRACT

Microanatomical studies on the genital system of *Esastigmatobius longitarsis* and *Craterostigmus tasmanianus* provide arguments to establish phyletic relationships between Henicopidae and Lithobiidae, and on the other hand between Craterostigmomorpha, Lithobiomorpha and epimorphic chilopods. Microanatomical studies on adult males of *Craterostigmus tasmanianus* indicate the presence of paired testes connected by the efferent canals to a single median deferens canal. The male genital system of *C. tasmanianus* is similar to that of the orders Scolopendromorpha and Geophilomorpha. The male genital system in *Esastigmatobius longitarsis* presents a single flagelliform median testis and two seminal vesicles. The testis is continued by a deferens canal which opens in the zone of the confluence of the two seminal vesicles. The genital tract is continued by two ejaculatory ducts, which open separately into the atrium. The glandular system of the male genital tract is composed of dorsal accessory glands, ventral accessory glands and atrial glands. In the single testis there is a unique type of spermatogenesis producing spermatocytes of large size. The female genital system, similar to that of Lithobiidae, is also described. The possible phyletic relationships of the family Henicopidae *s. st.* and the tribe Anopsobiini are discussed.

RÉSUMÉ

Données préliminaires sur l'anatomie du système génital mâle chez *Craterostigmus tasmanianus* (Craterostigmomorpha) et des systèmes génitaux mâle et femelle chez *Esastigmatobius longitarsis* (Henicopidae, Lithobiomorpha) (Chilopoda).

Des études d'anatomie, en microscopie optique, des individus mâles de *C. tasmanianus* indiquent la présence de paires de vésicules testiculaires reliées par des canaux afférents à un canal déférent central, impair. Le système génital mâle de *Craterostigmus* est similaire au système génital des ordres Scolopendromorpha et Geophilomorpha. Le système génital mâle chez *Esastigmatobius longitarsis* présente un seul testicule médian, flagelliforme et deux vésicules séminales. Le testicule est prolongé par un canal déférent allongé et contourné qui débouche dans la zone de confluence des vésicules séminales. Le système glandulaire du tractus génital mâle est formé de glandes accessoires dorsales, accessoires ventrales et atriales. Dans le testicule se déroule un type de spermatogenèse unique avec des spermatocytes de grande taille. On décrit aussi le système génital femelle de cette espèce qui est semblable au système génital femelle des Lithobiidae. La discussion finale concerne les relations phylogénétiques de la famille Henicopidae *s. str.* et de la tribu Anopsobiini.

PRUNESCU, C. C., MESIBOV, R. & SHINOHARA, K., 1996. — Preliminary data on the anatomy of the genital systems in *Craterostigmus tasmanianus* (Craterostigmomorpha) and *Esastigmatobius longitarsis* (Henicopidae, Lithobiomorpha) (Chilopoda). *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 341-346. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

INTRODUCTION

Genital systems are relatively well studied within the family Lithobiidae (cf. ATTEMS, 1926; PRUNESCU, 1964, 1965a; RILLING, 1968 ; LEWIS, 1981).

Many years after the description of the microanatomy of the female genital system in *Craterostigmus tasmanianus* was published (PRUNESCU, 1965b), we obtained new specimens of this species. Difficulties in fixing and preserving of this material as well as a disadvantageous sex ratio of this lot have not allowed us to make good quality dissections capable of clearing up the problem of the precise number of pseudometameric testicular vesicles. Taking into account that any positive data, even incomplete, dealing with the order Craterostigmomorpha are opportune and can be useful in this period of cladistic phylogeny, we propose the preliminary data presently at our disposal.

In the family Henicopidae, which presents an extra European distribution, the genital system in general does not yet seem to have been studied. We present microanatomical data on the genital system in *Esastigmatobius longitarsis*, as they appear from the study of the serial cross-sections of the posterior half of the body, in male and female individuals.

MATERIAL AND METHODS

Several individuals of *C. tasmanianus* were collected from Goderich Road (N.W. Tasmania) by R. MESIBOV at an altitude of 580 m, on 12 September, 1991. They were fixed in 3% glutaraldehyde, in cacodylat buffer, pH 7.4, for 4 days. The parts were then placed in 70% ethylic alcohol. After routine histological technique, paraffin-embedded material was sectioned at 6 µm and coloured with hemalum-eosine. Some adult male and female individuals of *E. longitarsis*, collected from Japan by K. SHINOHARA and fixed in 70% ethylic alcohol were studied using the same methods.

RESULTS

Genital system of Craterostigmus tasmanianus

The testicular system of *Craterostigmus tasmanianus* consists of several testicular vesicles placed one side and another of a deferens duct (Figs 1-4). Each testicular vesicle is an elongated and sinuous formation. It communicates with the central deferens duct by two other afferens ducts, one anterior and the other posterior.

The deferens duct is bifurcated, in the hind-gut area, into two ejaculatory ducts (Figs 5-6) which descend to the ventral region of the body and open into the male genital atrium. The two ducts of the dorsal accessory glands also open here. The two ducts of the ventral accessory glands open into an unpaired ventral duct, which in turn communicates with the genital atrium (Fig. 6). Both dorsal and ventral accessory glands are well-developed acinous glands.

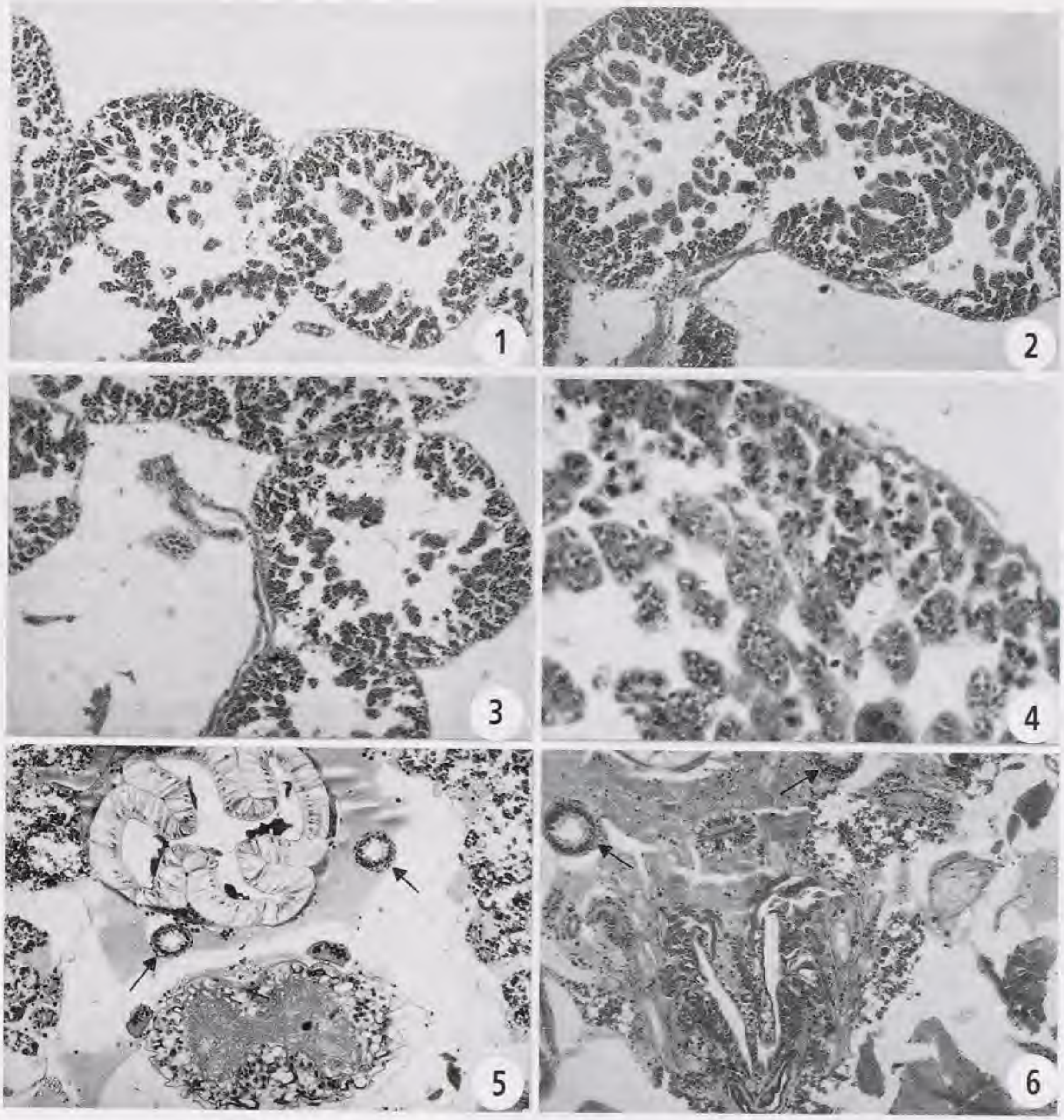
Male genital system of Esastigmatobius longitarsis

The testis is unpaired, tubular and elongated (Fig. 7). Towards the posterior end, the lumen of the testis narrows and takes on the aspect of a deferens duct (Fig. 8). In its caudal part, the deferens duct holds numerous spermatogonia and even small spermatocytes. These spermatocytes occur in different stages of cellular degeneration.

On the left and right sides of the testicle, there are elongated, tubular, seminal vesicles, situated dorsally relative to the medium intestine and closed at their anterior end like a glove finger. The two seminal vesicles join and immediately after their joining, in the medio-dorsal part of the resulting formation, the deferens duct of the testis opens (Fig. 9).

The genital tractus is continued by two ejaculatory ducts (Fig. 10) which descend by the posterior intestine. In their anterior part, the ejaculatory ducts are represented by two large, dilated tubes with thick walls consisting of a secretory cylindric epithelium. This epithelium synthesizes and secretes into the lumen a finely granulated eosinophil-rich secretion, mixed with numerous basophil granules. As these ducts descend in the ventral and caudal part of the body, their diameter grows smaller and the lumen narrows.

Source : MNHN, Paris



FIGS 1-3. — Sections through the testicular vesicles at the deferens canal level. Note the efferens canals and the deferens canal. x120.

FIG. 4. — Testicular vesicle (detail). Spermatogonia and spermatocytes are seen during the division process or at the beginning of the growth. x500.

FIG. 5. — Transverse section through the hind-gut region. The two ejaculatory canals (arrowed) can be seen between the hind-gut and a ventral nerve ganglion. x120.

FIG. 6. — Section through the male genital atrium. Ejaculatory canals (arrow). x160.

The single pair of dorsal accessory glands and the single pair of ventral accessory glands are acinous tubular glands. The ducts of the ventral accessory glands join (anteriorly) to form an unique duct which represents part of the genital atrium (Fig. 11). The ducts of the dorsal accessory gland also join, posteriorly, to form a single duct. It is continued by a cylindrical

Source : MNHN, Paris

structure which represents the central part of the genital atrium, also named the central duct of the atrium (Fig. 11).

The two ejaculatory ducts penetrate separately into a dorsal structure of the genital atrium (Fig. 12). The bottom of this structure consists of a glandular epithelium. The ejaculatory ducts open in the atrium caudally, after the central and the unique ducts of the ventral accessory glands join and open outwards. In the atrium, an acinous atrial gland forms caudally (Fig. 13).

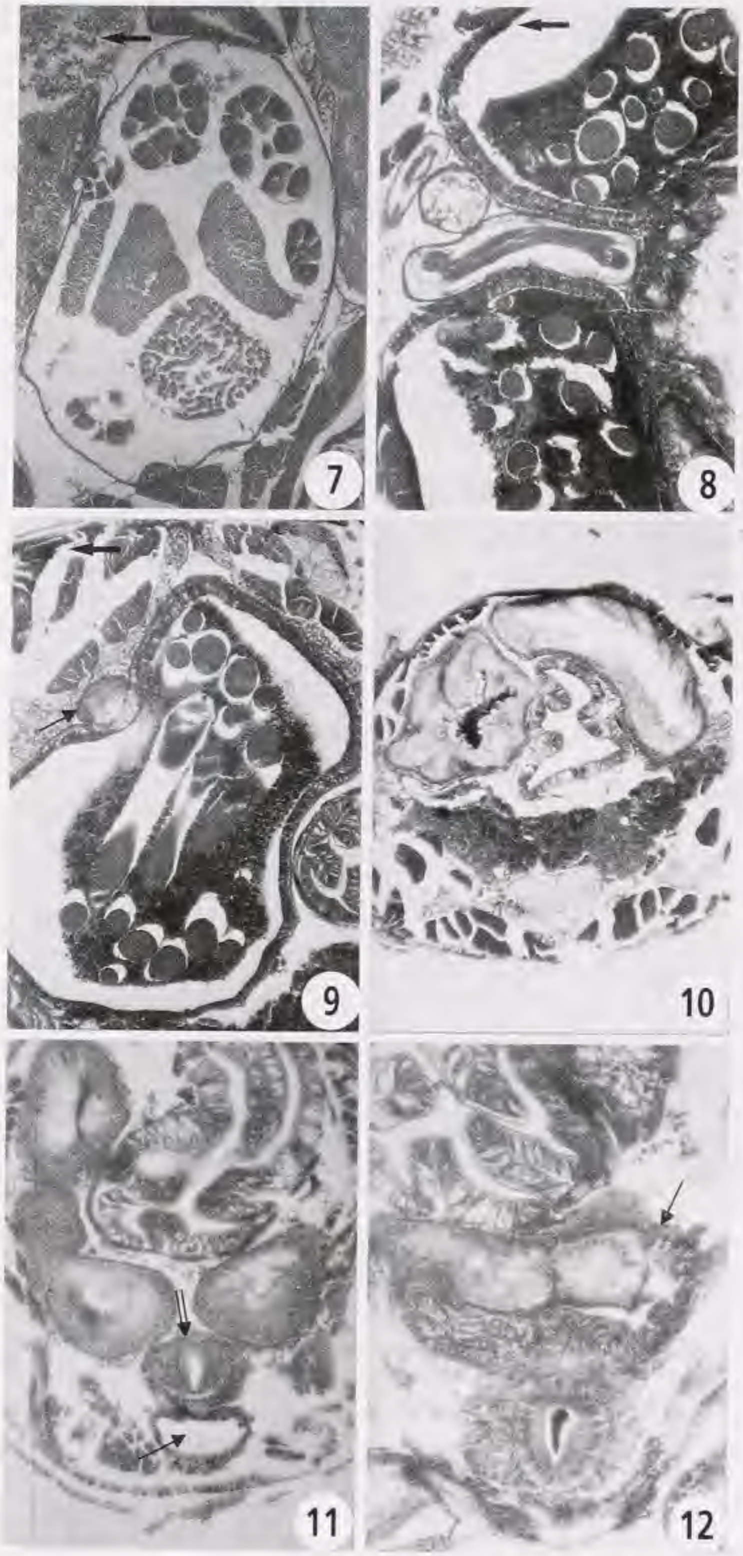


FIG. 7. — Transverse section through the single testes; it presents many groups of spermatocytes and fascicles of spermatozoa. x100. The thick arrow shows the top of the slide.

FIG. 8. — Transverse section through posterior extremity of seminal vesicles. Within these vesicles can be seen fascicles of spermatozoa and a granular secretory material. Between the seminal vesicles, many profiles of the deferens duct are visible. x90. The thick arrow shows the top of the slide.

FIG. 9. — Transverse section at the level of the joining of the two seminal vesicles; the deferens duct can be seen dorsally and the hind-gut ventrally. x 90. The thick arrow shows the top of the slide.

FIG. 10. — Transverse section at the level of the ejaculatory ducts. x60.

FIG. 11. — Transverse section through the ejaculatory ducts at the level of the genital atrium. Single arrow indicates the unique duct of the ventral accessory glands; double arrow the central duct of the atrium. x90.

FIG. 12. — Genital atrium at the level of the opening of the ejaculatory ducts (arrow). x140.

Source : MNHN, Paris

Female genital system of Esastigmatobius longitarsis

The female genital system consists of an elongated tubular ovary which is above or beside the mid-gut (Fig. 14). The caudal part of the ovary is continued by two oviducts which descend and surround the posterior intestine. A pair of large seminal receptacles (Fig. 15) communicates with the genital atrium by a narrow duct. It is surrounded by a sheath of circular muscles. The genital atrium is a large structure which presents, in its anterior part, a high epithelium surrounded by numerous glandular acini, the ducts of which open into the atrium (Fig. 16). In cross-section, the female genital atrium presents a V-shape. Each oviduct opens into the corresponding latero-dorsal end (Fig. 16). The ducts of ventral glands open separately through the latero-ventral walls of the atrium (Fig. 17). The ducts of the seminal receptacles wind several times in tight spirals, penetrate the dorsal wall of the atrium, and open into the terminal part of the atrium (Fig. 18). The dorsal accessory glands open at about the same level, through the latero-dorsal walls of the atrium.

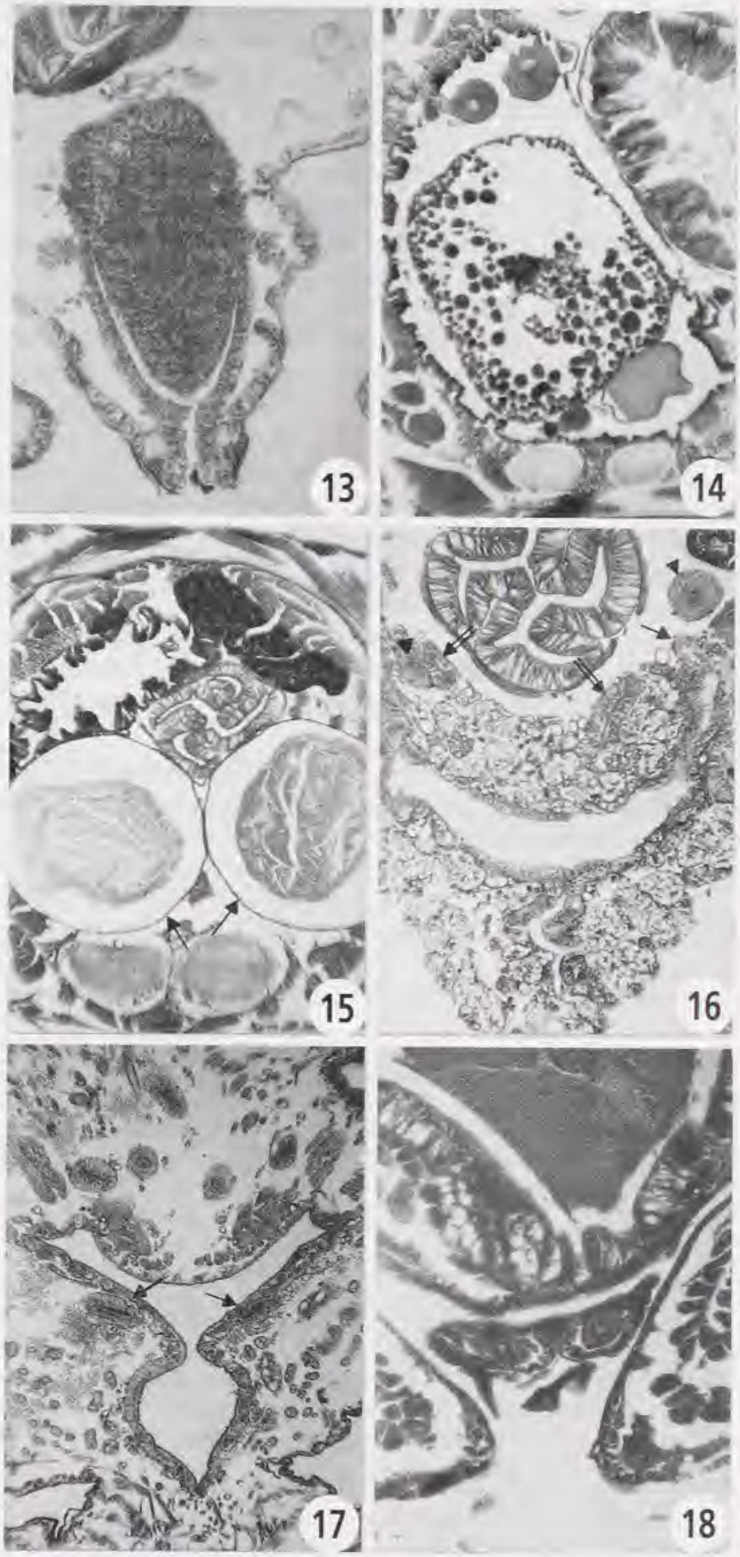


FIG. 13. — Acinous atrial gland. x140.
FIG. 14. — Transverse section through the ovary. x100.
FIG. 15. — Transverse section through the seminal receptacles (arrow). Inside of the receptacles are masses of spermatozoa. x60.
FIG. 16. — Transverse section through the anterior region of the genital atrium at the level of the opening of the oviducts. Arrow indicates oviduct, the arrowheads the ducts of the seminal receptacles, the double arrow the ducts of the accessory dorsal glands. x90.
FIG. 17. — Opening of the ducts of the ventral accessory glands (arrow). x90.
FIG. 18. — The terminal zone of the genital atrium. Opening of the ducts of the semi-receptacles. x200.

Source : MNHN, Paris

DISCUSSION

Our data on the testicular system of *Craterostigmus tasmanianus* do not allow us to specify the number of the vesicular testicles, That seems to be equal to or larger than two pairs. The testicular system in *C. tasmanianus* resembles that of epimorphic chilopods. We have to mention the missing of the seminal vesicles, characteristic for Lithobiomorpha. The fact that the larva of *C. tasmanianus* has 12 leg-bearing segments at its eclosion (MANTON, 1965) shows that this line detached from the main evolutionary line which linked anamorphic chilopods to epimorphic ones. It is known that *Craterostigmus* females take care of their eggs (LEWIS, 1981) as do all epimorphic chilopods. The presence of pseudometameric testes in a chilopod with 15 leg-bearing segments and many resemblances in its outer morphology and way of life with the epimorphic chilopods with an elongated body may appeared and evolved from ancestors with anamorphic features (PRUNESCU, 1969a).

The male genital system of *E. longitarsis* resembles that of Lithobiidae. Unlike the Lithobiidae, whose ejaculatory ducts join before opening in the atrium by an unique ejaculatory duct, those of Henicopidae have the ejaculatory ducts opening separately into the genital atrium. The presence of paired male genital tracts in some genera of Anopsobiini (Henicopidae) (PRUNESCU & JOHNS, 1969; PRUNESCU, 1992a), indicates the phyletic complexity of Henicopidae and supports the idea that they have retained numerous plesiomorphic features of the genital system. The existence of a male gonopod of 4 articles in all lines of Henicopidae also argues for the primitiveness of this group but, at the same time, covers its heterogeneity. The presence in the deferens duct of the single testicle of small elements belonging to an abortive spermatogenesis, suggests a closeness of this phenomenon to the microspermatogenesis in the deferens duct-microtestes in *Scutigera* (FAHLANDER, 1938; PRUNESCU, 1969b, 1992b) and Anopsobiidae (PRUNESCU & JOHNS, 1969). The female genital system presents less significant morphological differences in comparison with that of in Lithobiidae.

ACKNOWLEDGMENTS

The two original papers which constituted the present work have been revised and successfully unified by Dr J.-J. GEOFFROY (Editor). We deeply thank him for this benefic effort.

REFERENCES

ATTEMS, C., 1926. — Chilopoda. *In* : W. KÜKENTHAL, *Handbuch der Zoologie. Progoneata. Chilopoda. Insecta*. Berlin und Leipzig, W. de Gruyter & Co. : 239-402.

FAHLANDER, K., 1938. — Beiträge zur Anatomie und systematischen Einteilung der Chilopoden. *Zool. Beidr. Upps.*, **17** : 1-148.

LEWIS, J. G. E., 1981. — *The biology of Centipedes*. Cambridge, Cambridge Univ. Press, 475 pp.

MANTON, M. S., 1965. — The evolution of arthropod locomotory mechanisms, 8. *Zool. J. Linn. Soc.* , **46** : 251-483.

PRUNESCU, C. C., 1964. — Anatomie microscopique du système génital mâle des Lithobiidés. *Rev. Roum. Biol. (Zool.)*, **9** : 101-104.

PRUNESCU, C. C., 1965a. — Contribution à l'étude anatomique et anatomo-microscopique du système génital femelle de l'ordre Lithobiomorpha. *Rev. Roum. Biol. (Zool.)*, **10** : 11-16.

PRUNESCU, C. C., 1965b. — Les systèmes génital et trachéal de *Craterostigmus* (Chilopoda). *Rev. Roum. Biol. (Zool.)*, **10** : 309-312.

PRUNESCU, C. C., 1969a. — Quelle est la place occupée par *Cermatobius*, *Craterostigmus* et *Plutonium* dans la phylogénie des Chilopodes? *Bull. Mus. natl. Hist. nat. Paris*, **41, suppl. 2** : 112-115.

PRUNESCU, C. C., 1969b. — Le système génital mâle de *S. coleoptrata* (Notostigmophora, Chilopoda). *Rev. Roum. Biol. (Zool.)*, **14** : 185-190.

PRUNESCU, C. C., 1992a. — The genital system in *Dichelobius* (Anopsobiidae, Lithobiomorpha, Chilopoda). *Ber. nat.-med . Verein Innsbruck*, **suppl.10** : 87-91.

PRUNESCU, C. C., 1992b. — The beginning of double spermatogenesis in *Scutigera coleoptrata*. *Ber. nat.- med . Verein Innsbruck*, **suppl. 10** : 93-97.

PRUNESCU, C. C. & JOHNS, M., 1969. — An embryonic gonad in adult males of *Anopsobius neozelandicus* Silv. (Chilopoda). *Rev. Roum. Biol. (Zool.)*, **14** : 407-409.

RILLING, G., 1968. — *Lithobius forficatus*. *In* : *Grosses Zoologisch Praktikum*, part. 13 b. Stuttgart, Fischer.

Source : MNHN, Paris

On Some Structural Abnormalities in *Dignathodon microcephalum* (Lucas, 1846) and their Possible Significance

Francisco J. SANTIBAÑEZ & *Andrès* GARCIA RUIZ

Departamento de Biología Animal I (Entomología), Facultad de Ciencias Biológicas, Universidad Complutense
E-28040-Madrid, Spain

ABSTRACT

Some specimens of *Dignathodon microcephalum* (Lucas, 1846) with some structural abnormalities in the antennal articles and the last pair of legs are described. There is no indication of damage or regeneration in these specimens and we presume that these are developmental abnormalities.

RÉSUMÉ

Signification de quelques anomalies de structure chez *Dignathodon microcephalum* (Lucas, 1846).

On a étudié des spécimens de *Dignathodon microcephalum* présentant des anomalies de structure sur les articles antennaires et la dernière paire de pattes. L'absence de toute trace de dommage ou de régénération chez les individus observés amènent à penser qu'il s'agit d'un développement anormal.

INTRODUCTION

Among the large number of centipedes we have studied during the last few years we have found some specimens with abnormal structures. MINELLI & PASQUAL (1986) only found three types of abnormal structures on centipedes: spiral segmentation, mutation of a structure into another and branched appendix.

According to LEWIS (1987) some anomalous structures in centipedes may not fit into MINELLI & PASQUAL's classification (1986) because in most of the cases the anomalous structures are due to problems in the animal development or to structural regeneration after damage.

DESCRIPTION

Abnormal size of left antenna

In a female of *Dignathodon microcephalum* collected at Moral de Calatrava (Ciudad Real) on 6-IV-1986 the antennae are of different sizes; both have all the antennal articles but the left antenna is smaller than the right one because from the sixth to the penultimate article they are

SANTIBAÑEZ, F. J. & GARCIA RUIZ, A., 1996. — On some structural abnormalities in *Dignathodon microcephalum* (Lucas, 1846) and their possible significance. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 347-349. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

smaller than the corresponding articles of a normal antenna. The last article is of normal size (Fig. 1).

Abnormal size of the last antennal article on the right antenna on a female

On a female of *Dignathodon microcephalum* collected in Talamanca del Jarama (Madrid), on 30-III-1988 the last antennal article on the right antenna is three times larger than its left equivalent (Fig. 2). This specimen shows no sign of damage and we think that the bigger size of the right last antennal article is due to an abnormal development.

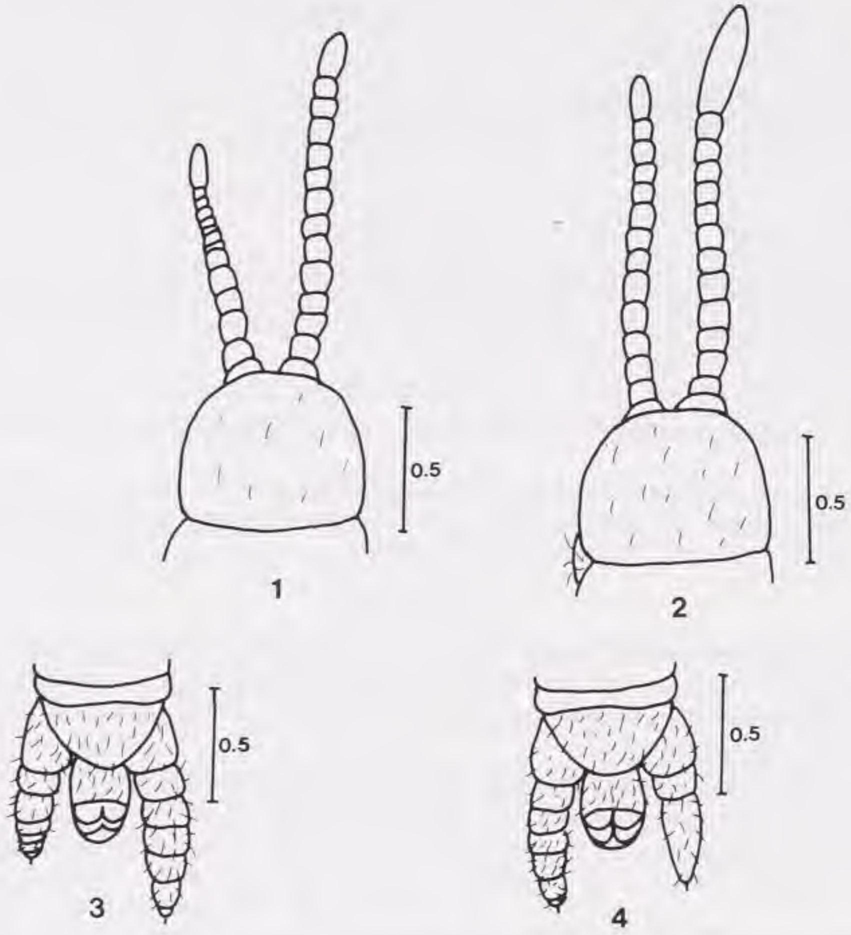


FIG. 1. — *Dignathodon microcephalum* (Lucas, 1846). Head and antennals dorsal view.
FIG. 2. — *Dignathodon microcephalum* (Lucas, 1846). Head and antennals dorsal view.
FIG. 3. — *Dignathodon microcephalum* (Lucas, 1846). Last segment. Ventral view.
FIG. 4. — *Dignathodon microcephalum* (Lucas, 1846). Last segment. Ventral view.

Abnormal size of the right leg on the last pair of legs

On a female of *Dignathodon microcephalum* collected at Moral de Calatrava (Ciudad Real) on 2-V-1987 the legs of the last pair were of different size. In both legs all articles are present but the right leg is smaller than the left: from the fourth article on, the length of the articles is lesser than the size of the corresponding (Fig. 3).

Source : MNHN, Paris

LEWIS (1988) described a similar case in a specimen of *Tygarrup javanicus* (Attems 1907), where the left leg was smaller than the right one due to the different sizes of the articles.

On the aforementioned specimen there is no sign of damage. We think that the smaller size of the articles on the right leg of the last pair of legs is due to abnormal development.

Abnormal development of the last four articles on the last left leg

On a female of *Dignathodon microcephalum* collected at Talamanca del Jarama (Madrid) on 30-III-1988 the last four articles on the last left leg are not articulated instead there is a bigger article that would fit with the fusion of the last four articles, because the size of the two legs is the same (Fig. 4).

On the aforementioned specimen there is no sign of damage. We think that this fusion of the last four articles is due to abnormal development on the appendage.

In conclusion, the four cases of abnormal structures studied seem really due to abnormal development of the articles on the respective appendage, because on none of the four specimens is there sign of damage. Because the anomaly is always based on the legs it is reasonable to think that this is due to their different development.

REFERENCES

LEWIS, J. G. E., 1987. — On some structural abnormalities in *Lithobius* and *Cryptops* (Chilopoda) and their possible significance. *Bull. Gr. Brit. Myriapod*, **4** : 3-6.

LEWIS, J. G. E., 1988. — *Tygarrup javanicus* (Attems) a Geophilomorph Centipede new to the British Isles. *Bull. Gr. Brit. Myriapod*, **5** : 3-10.

MINELLI, A. & PASQUAL, C., 1986. — On some abnormal specimens of Centipedes. *Lavori - Soc. Ven. Sc. Nat.*, **11** : 135-141.

Source : MNHN, Paris

Source : MNHN, Paris

Developmental Trends in the Post-Embryonic Development of Lithobiomorph Centipedes

Alessandro MINELLI, *Enrico* NEGRISOLO & *Giuseppe* FUSCO

Dipartimento di Biologia, Università di Padova, I-35121 Padova, Italy

ABSTRACT

The problem of comparing individual developmental stages of related species undergoing a different number of moults is tentatively settled by taking as developmental time units both major developmental periods, the first being between hatching and the transition from the last larval to the first postlarval stage, and the second between the first postlarval stage and the first mature stage. On such a re-scaled developmental schedule, the developmental trajectories of several characters in different species are studied, based on ANDERSSON's (1979) data. This analysis revealed extensive heterochrony, as did further comparisons of metric and meristic characters in mature specimens belonging to 62 species, with adult length ranging from 6 to 35 mm.

RÉSUMÉ

Modalités du développement post-embryonnaire des chilopodes lithobiomorphes.

Afin de résoudre le problème de la comparaison entre les stades de développement d'espèces présentant un nombre différent de mues, les auteurs utilisent en tant qu'unités temporelles les deux étapes fondamentales du développement : d'une part la phase allant de l'éclosion jusqu'au passage des stades larvaires aux stades post-larvaires, d'autre part la phase allant du premier stade post-larvaire jusqu'à la maturité sexuelle. La comparaison des trajectoires ontogénétiques de plusieurs caractères chez différentes espèces (données d'après ANDERSSON, 1979) révèle plusieurs cas d'hétérochronie. D'autres hétérochronies sont mises en évidence par la comparaison de plusieurs caractères métriques et méristiques entre des exemplaires adultes appartenant à 62 espèces, pour lesquels la longueur varie de 6 à 35 mm.

INTRODUCTION

The overall uniformity of body structure within all recent Lithobiomorpha, and especially within *Lithobius* s.l., where a great many species just seem to be "minor variations on a common theme", provides the scope for investigations of structural and morphogenetic constraints in the evolution of form. However, current knowledge of post-embryonic development of lithobiomorph centipedes is still in its descriptive phase; cf. especially the detailed studies of ANDERSSON (1979, and literature cited therein). Many additional, even basic aspects still need investigation, but we think that many insights, at least of a qualitative nature, can be obtained from a careful consideration of the extant evidence.

MINELLI, A., NEGRISOLO, E. & FUSCO, G., 1996. — Developmental trends in the post-embryonic development of Lithobiomorph Centipedes. *In:* GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 351-358. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

MATERIALS AND METHODS

We have mostly relied on literature data, but for the measures of individual podomeres in legs 1-15, we have studied *L. microps* Meinert (a female from Italy: Miogliola (AL)) and *L. forficatus* (Linnaeus) (a male from Italy: Bosco della Mesola (FE)). Two (a, b) main data bases have been collected: (a) head length (HL), body length (BL), number of ocelli (OC), number of antennomeres (AN), number of coxal pores (CP), number of coxosternal teeth (CT), number of setae on the first genital sternite of the male (SGM), id. of the female (SGF), in each post-embryonic stage of *Lithobius forficatus* (Linnaeus, 1758), *L. erythrocephalus* C. L. Koch, 1847, *L. melanops* Newport, 1845, *L. crassipes* L. Koch, 1862, *L. microps* Meinert, 1868, *L. calcaratus* C. L. Koch, 1844, *L. curtipes* C. L. Koch, 1847 and *L. tenebrosus* Meinert, 1872 (data compiled from ANDERSSON, 1979); (b) BL, OC, AN, CP, CT, total number of spines on the legs of one side of the animal (ST) and plectrotaxy (distribution of the individual spines on all pairs of legs) in the adults of the 62 species listed in the Appendix (data compiled from BROLEMANN, 1930; EASON, 1964; MATIC, 1966; ANDERSSON, 1979).

As for the methods, the less trivial points are the re-scaling of ontogenetic stages onto a normalized x-axis, as justified in the next section and explained also in the legend to Figure 1, and the standardization of the values of BL, OC, AN, CP, CT and ST before using them in multivariate analysis (principal components).

RESULTS

Comparability of ontogenetic stadia

When comparing the ontogenetic stadia of different, although closely related, arthropod species, the first question to answer is which stage of species B, if any, is more correctly and meaningfully comparable with a given stage of species A. Simply referring to the ordinal number of the stage (i.e., to the number of moults the animal has undergone) does not seem to be safe, because of the different number of stages that A and B may possibly go through before getting maturity, or during their whole life. We could even be faced with intraspecific variation in the number of post-embryonic stages. One of us (MINELLI, 1992) had already looked for a possible application to centipedes of GRANDJEAN's (1951) concept of *stase*, but could not find a fixed set of structurally distinct stages, independent from the number of moults occurring between any two of them.

We believe that only three points, along the post-embryonic development of all lithobiomorphs, can be more or less safely compared across species. These are the first larval stage (L0 in ANDERSSON's terminology), the first post-larval stage, i.e. the first stage with the full complement of segments and legs (PL1) Δ, and the first mature stage. The identification of the onset of maturity is not easy to assess in objective terms. For the species whose developmental schedules we have compared, we have simply accepted, for operational reasons, the estimates of maturity as given by ANDERSSON (1979), although his assessments were derived (but for *L. forficatus*) from comparative guesses rather than from objective, e.g. histological, proofs.

On this basis, we have re-scaled the post-embryonic stages of all species onto a common scale. We have dealt separately with the two intervals, the first between L0 and PL1, the second between PL1 and the first (guessed) mature stage (Fig. 1). For the species under study, this causes no relative changes between hatching and PL1, because the number of larval stages is always the same, whereas the individual post-embryonic stages of the different species account for different percentages of the normalized development. Some characters, e.g. head length, follow similar ontogenetic trajectories in all species, but others are subjected to heterochrony, at least for some species. Ontogenetic trajectories for ocelli start at different points, but subsequently evolve in comparable ways. In still other cases, as for the setae of first genital sternite in both sexes, heterochrony is given by the different speed of comparable ontogenetic changes that start at the same time. Again, as for the number of antennomeres, the first steps are the same in all species under comparison, but their further increase goes on at different speed; however, the different trajectories of antennomeres in *L. calcaratus* (or in *L. forficatus*) and *L tenebrosus* coincide again at the end. The passage from larval to post-larval stages seems to be a major change only for those characters whose phenotypic expression requires the presence of

Source : MNHN, Paris

fully developed segments XII and following (e.g., the number of setae on first genital sternite); and that, not for all species.

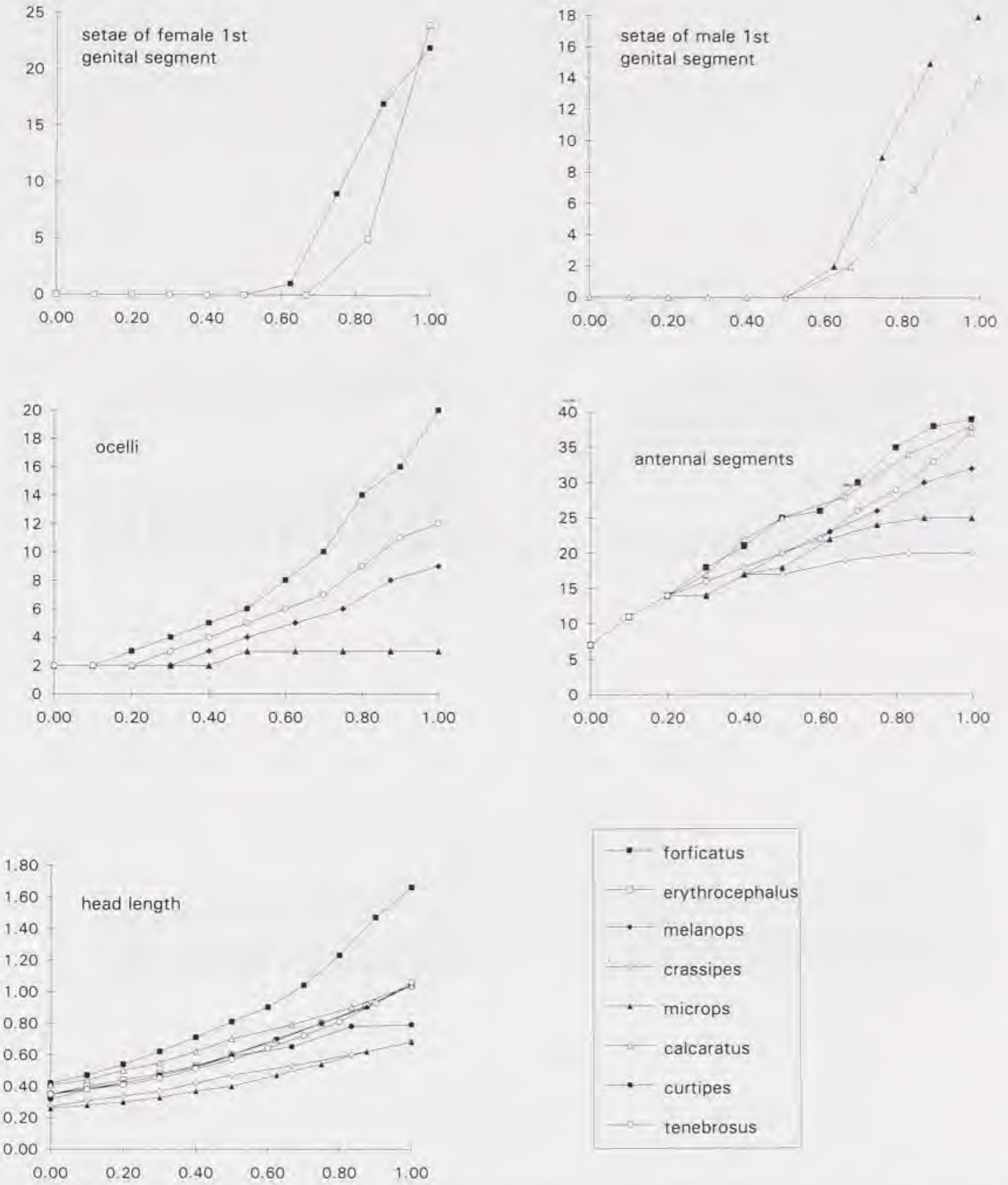


FIG. 1. — Ontogenetic trajectories for individual characters in selected *Lithobius* species. Data after ANDERSSON (1979). Horizontal axis represents normalized post-embryonic development, with first larval stage (L0) and first mature stage (guessed), respectively, at the two ends of the scale; mid-point of the x axis corresponds to PL1. Individual points along the trajectories refer to the individual post-embryonic stages, whose number before maturity is different in the different species. Head length in mm.

Source : MNHN, Paris

Comparisons of mature representatives of species of different size

Further comparisons have involved a comparable (mature) stage of 62 species (see Appendix) ranging in length from 6 to 35 mm. We have tried to identify the occurrence of coherent trends of variation of different structural traits, as well as the independence of other traits.

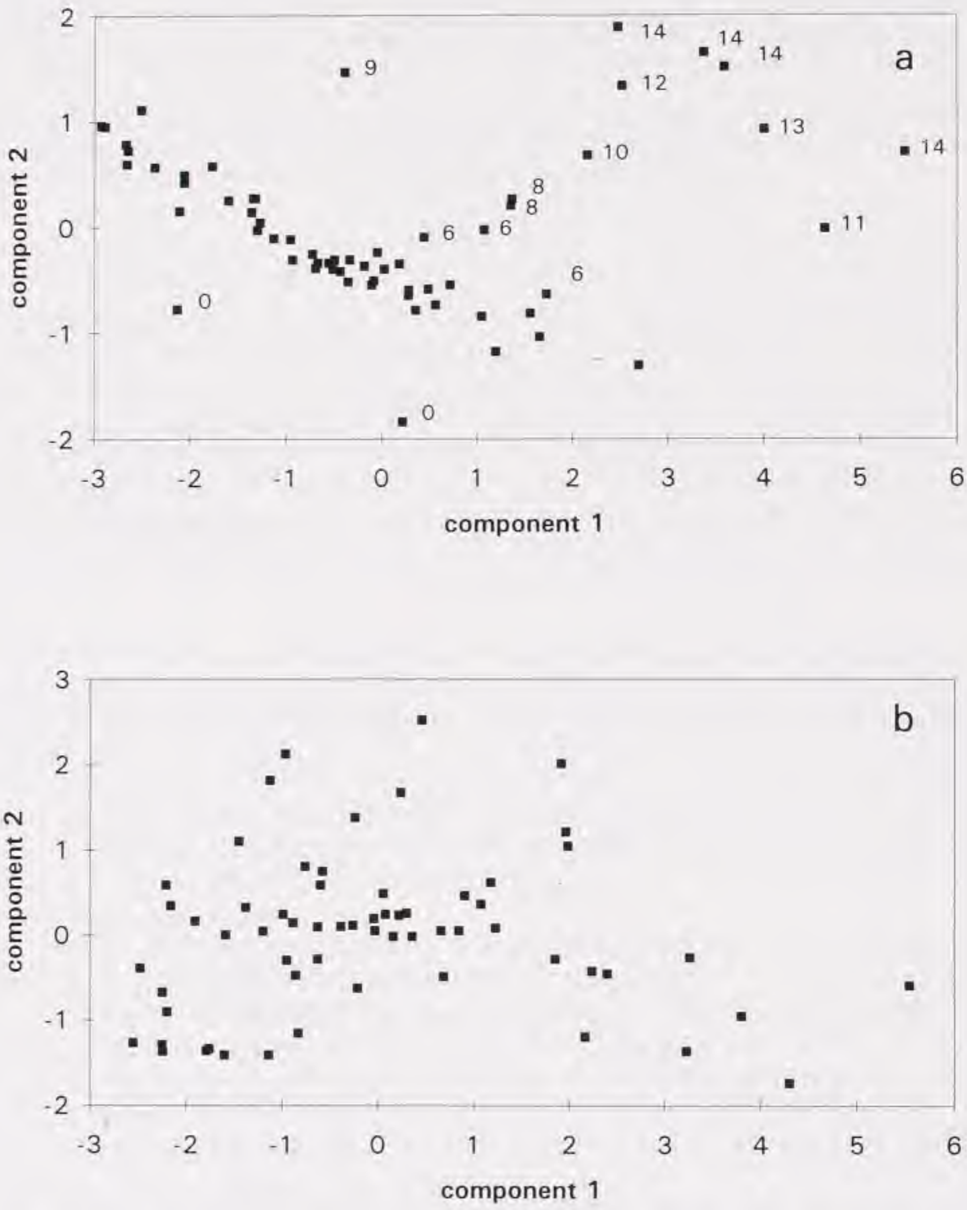


FIG. 2. — Scatter plot of the 62 *Lithobius* species listed in the Appendix onto the plane of principal components 1 and 2, the original variables being in (a) BL, OC, CP, CT and ST, in (b) BL, OC, CP, CT and AN. In (a), the percentual contributions of the first two principal components to total variance are, respectively, 72.6 and 11.5; in (b), the corresponding values are 64.0 and 18.0. In (a), the numbers within the plot identify the average number of CT; squares without numbers are for the species with CT=4.

Source : MNHN, Paris

If we place the 62 species in the morphospace identified by the following 5 variables: BL, OC, CP, CT, ST in a plot of principal components 1 and 2 (Fig. 2a), we see a very coherent distribution, with points seemingly arranged in parallel rows, each of them corresponding to an "isoodont line", along which are aligned the species with the same number of coxosternal teeth.

The number of antennomeres does not behave as these five characters. Figure 2b shows the disruptive effect of substituting AN for ST in the set of original variables. That means, that the antennae are not subjected to the same constraints as the other four variables.

Thus, these interspecific comparisons provide further evidence for heterochrony, because of the different variation of individual characters with size at maturity.

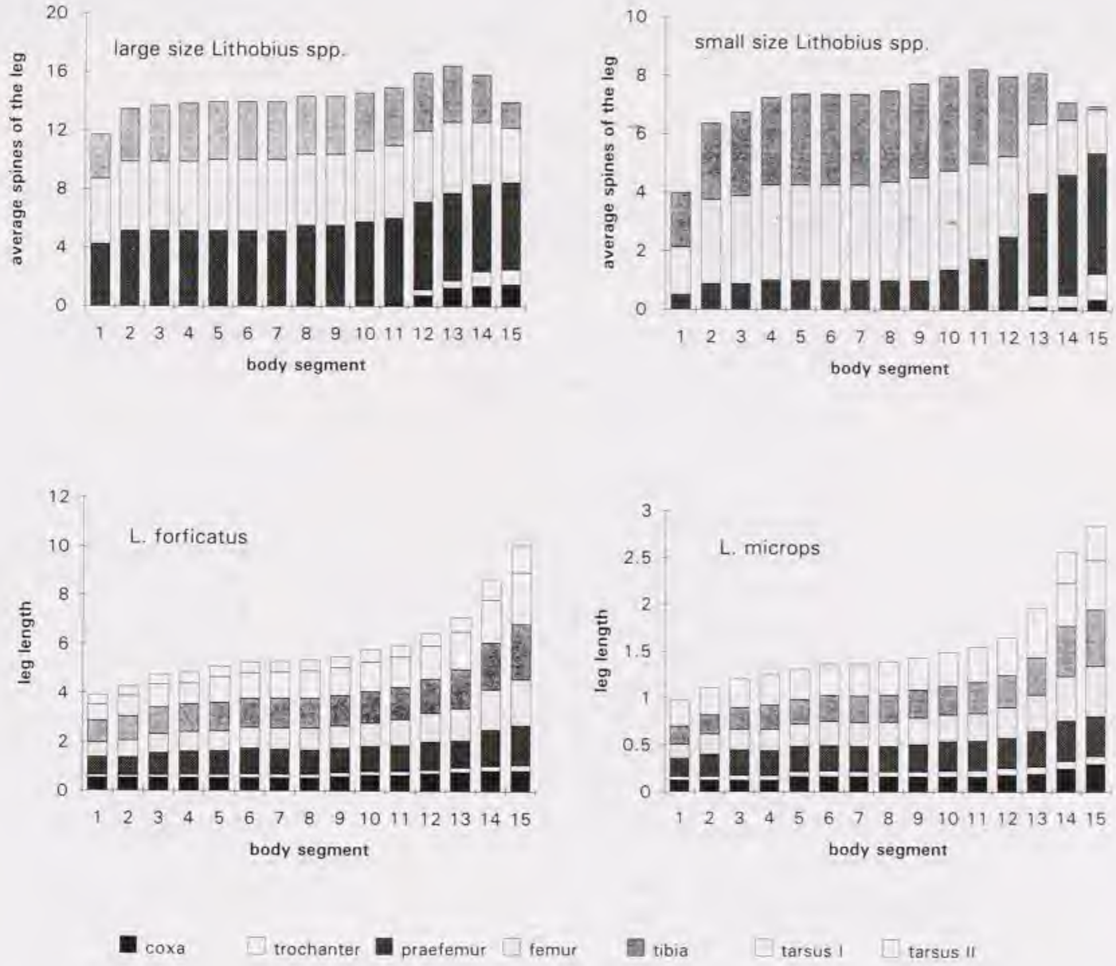
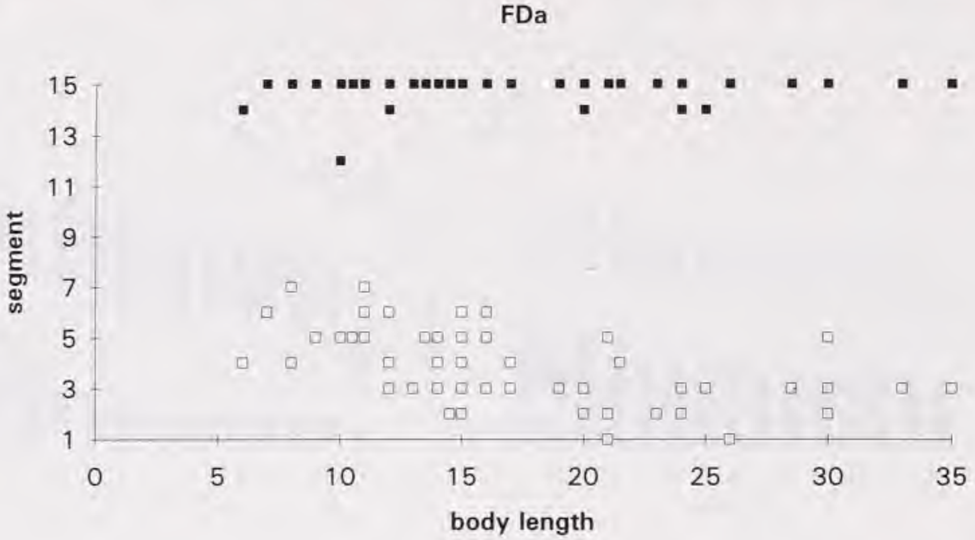


FIG. 3. — Plectrotaxy and leg length. Bar diagrams in the upper row give the mean number of spines per podomere (coxa to tibia) per leg (I to XV) in the eight largest species listed in the Appendix (left) and in the seven smallest species of the same list (right). Bar diagrams in the under row give the length (mm) of the individual podomeres in each leg (I to XV) in one individual of a large species (left: *Lithobius forficatus*, male) and in one individual of a small species (right: *Lithobius microps*, female).

Source : MNHN, Paris

Size at maturity has also an effect over the segmental pattern of distribution of leg spines. In the small species (Fig. 3, upper row, right), the average number of spines per leg increases steeply from segment I to segment III, goes on with trifling differences until segment IX or X, peaks at XI, then slowly decreases, whereas in the large species (Fig. 3, upper row, left) a "near-saturation" is soon reached on leg II. The prefemur is most responsible for the changes in the number of spines throughout the segments.

Changes in spinulation of the proximal podomeres (coxa and trochanter) of all species and especially of the prefemur of small species parallel leg length changes along the body. However, leg length profiles are not different in small vs. large species (Fig. 3, under row).



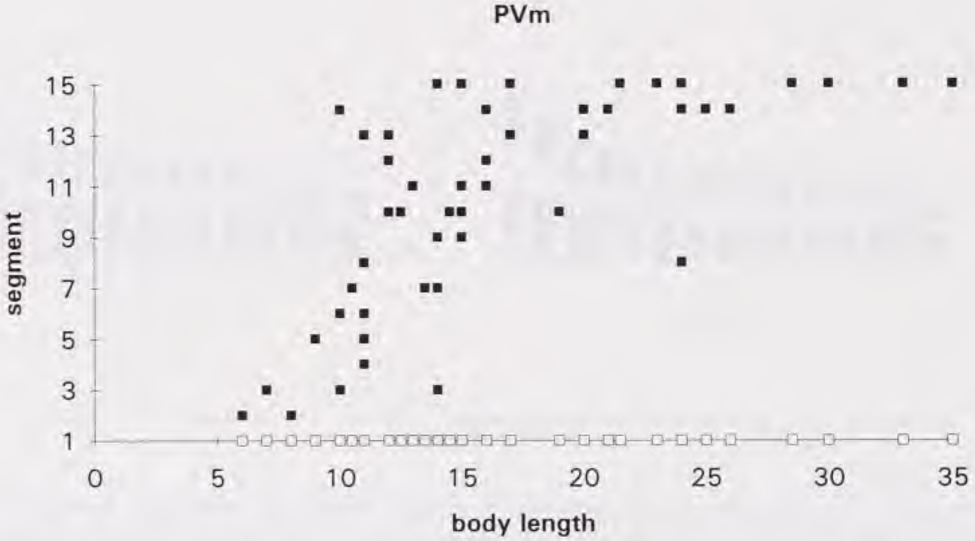


FIG. 4. — Range of segments where the anterior dorsal spine of the femur (FDa, above), and the median ventral spine of the prefemur (PVm, below) occur, in typical representatives of each of the 62 species listed in the Appendix, plotted against average body length (mm). Full squares mark the most anterior segment, empty squares the last segment with the given spine.

Source : MNHN, Paris

Leg size and leg spinulation could be both explained as controlled, over the whole trunk length, by at least two factors acting from centers at both ends of the body.

For those positions where the number of pairs of legs with spines increases with the size of the animal at maturity, two main patterns are observed, one centered in the fore trunk and another centered in the hind trunk (Fig. 4).

DISCUSSION

While acknowledging that a definitive evaluation of evolutionary trends, including heterochronies, necessitates a sound and detailed phylogenetic background, such as we cannot yet provide for lithobiids, we believe that our preliminary comparisons of structural and developmental trends are already suggestive of an interesting interplay of strong constraints - such as those keeping together, across a large number of species, body size, number of ocelli, spinulation and number of coxal pores - with the largely independent variation of other traits; at the same time, a great deal of specific differences seem to be easily (we would dare to say: *inexpensively*) obtained by fine-tuning starts, speeds and end points of fundamentally identical processes.

APPENDIX

List of the species whose adult traits were compared (cf. Fig. 2). Data on these species, which are generally listed here under the names used by the authors, were compiled from ANDERSSON (1979), BROLEMANN (1930), EASON (1964), MATIC (1966). Species marked with (L) or (S) are the large or small species considered for the analysis of plectrotaxy as in Figure 3.

Lithobius (*Monotarsobius*) *aeruginosus* L. Koch, 1862
L. agilis pannonicus Loksa, 1948
L. allotyphlus Silvestri, 1908
L. aulacopus Latzel, 1880,
L. (*M.*) *baloghi* Loksa, 1947 (S)
L. (*M.*) *biunguiculatus* Loksa, 1947 (S)
L. borealis Meinert, 1872
L. bulgaricus Verhoeff, 1925 (L)
L. (*M.*) *burzenlandicus* Verhoeff, 1931 (S)
L. calcaratus C. L. Koch, 1844
L. castaneus Newport, 1844 (L)
L. cavernicola Fanzago, 1877
L. (*M.*) *crassipes* L. Koch, 1862
L. crypticola Ribaut, 1926
L. (*M.*) *curtipes* C. L. Koch, 1847
L. cyrtopus Latzel, 1880
L. (*Thracolithobius*) *dacicus* Matic, 1959
L. decapolitus Matic *et al.*, 1962
L. (*M.*) *dobrogicus* Matic, 1962 (S)
L. (*Dacolithobius*) *domogledicus* Matic, 1961
L. (*M.*) *duboscqui* Brölemann, 1896
(=*L. microps* Meinert, 1868) (S)
L. (*M.*) *dudichi* Loksa, 1947 (S)
L. erythrocephalus C. Koch, 1847
L. fagniezi Ribaut, 1926
L. forficatus (Linnaeus, 1758) (L)
L. inermis L. Koch, 1856
L. (*Th.*) *inexpectatus* Matic, 1962
L. lapidicola Meinert, 1868
L. latro Meinert, 1872
L. lucifugus L. Koch, 1862
L. luteus Loksa, 1947
L. matici matici Prunescu, 1966 (L)
L. melanops Newport, 1845
L. (*M.*) *microps* auct. nec Meinert, 1868
L. mutabilis L. Koch, 1862
L. muticus C.L. Koch, 1847
L. nicoeensis (Brölemann, 1904)
L. nigrifrons Latzel, 1880
L. nodulipes Latzel, 1880
L. parietum Verhoeff, 1899 (L)
L. pelidnus Haase, 1888
L. peregrinus Latzel, 1880
L. piceus L. Koch, 1862
L. pilicornis Newport, 1844 (L)
L. punctulatus vasconicus (Chalande, 1905) (L)
L. (*M.*) *pustulatus* Matic, 1964
L. ribauti Chalande, 1907
L. (*M.*) *sciticus* Prunescu, 1965
L. silvivagus Verhoeff, 1925
L. speluncarum Fanzago, 1877
L. (*M.*) *subterraneus* Matic, 1962 (S)
L. tricuspis Meinert, 1872
L. troglodytes scutigeropsis Brölemann, 1930
L. typhlus Latzel, 1886
L. variegatus Leach, 1817
Harpolithobius anodus dentatus Matic, 1957
H. banaticus Matic, 1961 (L)
H. intermedius Matic, 1958
H. oltenicus Negrea, 1962
H. radui Matic, 1955
H. triacanthos Matic, 1964
H. tridentatus Matic, 1962

Source : MNHN, Paris

ACKNOWLEDGEMENTS

This research was supported by grants of the Italian National Research Council (CNR) and the Italian Ministry of University and Scientific and Technical Research (MURST) to A. MINELLI.

REFERENCES

ANDERSSON G., 1979. — Taxonomical studies on the post-embryonic development in *Lithobius*, with a brief comparison with *Lamyctes* (Chilopoda: Lithobiomorpha). Ph. Thesis, Göteborg, Department of Zoology, Göteborg Univ.

BROLEMANN, H. W., 1930 — *Éléments d'une faune des Myriapodes de France : Chilopodes*. Toulouse, Imprimerie Toulousaine, 405 pp.

EASON, E. H., 1964. — *Centipedes of the British Isles*. London, Frederick Warne & Co, 294 pp.

GRANDJEAN, F., 1951. — Les relations chronologiques entre ontogenèse et phylogenèse d'après les petits caractères discontinus des Acariens. *Bull. biol. France Belg.*, **85** : 269-292.

MATIC, Z., 1966. — *Fauna Republicii Socialiste Romania. Clasa Chilopoda Subclasa Anamorpha., Vol VI, Fasc. 1.* Bucuresti, Acad. Rep. Soc. Romania. 267 pp.

MINELLI, A., 1992. — Towards a new comparative morphology of myriapods. *Ber. nat.-med. Verein Innsbruck*, **suppl. 10** : 37-46.

Source : MNHN, Paris

Étude de la reproduction et du développement post-embryonnaire de *Lithobius pilicornis* Newport, 1844 (Chilopoda, Lithobiomorpha)

Antoni SERRA *& Maria Carme* MIQUEL

Departament de Biologia Animal, Facultat de Biologia, Universitat de Barcelona, Avda. Diagonal, 645
E-08028 Barcelona, Espagne

RÉSUMÉ

Dans le cadre de l'étude du développement post-embryonnaire de *Lithobius pilicornis*, un élevage de couples d'adultes a été réalisé en laboratoire afin d'obtenir des spécimens d'âge connu. Aucun des mâles n'a déposé de spermatophore mais les femelles, fécondées avant la capture, ont pondu de nombreux œufs. Ces expériences ont permis d'observer la ponte, l'éclosion, la mue et l'alimentation des stades juvéniles. Le grand nombre de larves de différents stades de développement obtenu ainsi a permis d'étudier la variabilité des caractères morphologiques. Les critères suivants ont été utilisés afin de définir les différents stades : taille, spinulation des pattes, nombre d'appendices ambulatoires, d'ocelles, d'articles antennaires, de dents du coxosternum forcipulaire, de pores coxaux et d'appendices génitaux.

ABSTRACT

Reproduction and post-embryonic development of *Lithobius pilicornis* Newport, 1844 (Chilopoda, Lithobiomorpha).

The main goal of this work was to study the post-embryonic development of *Lithobius pilicornis*. Laboratory rearing was carried out in order to provide specimens of known age. No male of the several couples reared lay spermatophores, but the females spawned numerous eggs (they were already fertilized when captured). This experiment allowed observations on the egg-laying, hatching, moulting and feeding of the juvenile stages reared in laboratory. The large number of larvae in different developmental stages obtained in this way allowed the study of the variability of their morphological features. The following characters were used in order to establish the different post-embryonic developmental stages: size, number of ambulatory appendages, ocelli, antennal articles, forcipule coxosternum teeth, coxal pores, spinulation and genital appendages.

INTRODUCTION

Le processus de développement postembryonnaire des chilopodes lithobiomorphes comporte l'existence de différents stades dont les caractères diffèrent souvent de ceux qu'on trouve chez l'adulte. Ce fait rend difficile l'identification spécifique des exemplaires non adultes.

Les auteurs intéressés, jusqu'à ce jour, par l'étude et la description des différents stades du développement post-embryonnaire des espèces appartenant à l'ordre Lithobiomorpha sont en nombre réduit. Il faut toutefois citer des auteurs comme VERHOEFF (1905), BROLEMANN

SERRA, A. & MIQUEL, M. C., 1996. — Étude de la reproduction et du développement post-embryonnaire de *Lithobius pilicornis* Newport, 1844 (Chilopoda, Lithobiomorpha). *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 359-364. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

(1930), MURAKAMI (1958, 1960), EASON (1964, 1970), SCHEFFEL (1969) et surtout les nombreux travaux d'ANDERSSON (1976, 1978a, 1978b, 1979, 1980, 1981a, 1981b, 1982a, 1982b, 1983, 1984a, 1984b, 1990) sur la description et la caractérisation du développement des différentes espèces de lithobiomorphes.

Dans ce travail, les caractéristiques morphologiques sont décrites pour les différents stades larvaires de *Lithobius pilicornis* Newport, 1844. Afin d'obtenir un nombre élevé d'exemplaires d'âge connu, on a fait se reproduire cette espèce en captivité, ce qui nous a permis d'observer et remarquer maints aspects de sa biologie de reproduction.

MATÉRIEL ET MÉTHODES

Les individus de *Lithobius pilicornis* utilisés pour notre étude ont été capturés sur la Serra de Roqueroles, La Pena, Poblet (Tarragona), le 1.X.1990 et le 6.IV.1992. Au cours de la collecte effectuée en 1990 on a obtenu 8♂ et 19♀, qui ont été séparés en 6 couples et 15 individus (2♂ et 13♀) isolés chacun dans une boîte en matière plastique de 12 x 8 x 6 cm, dont le fond a été recouvert avec une couche de 4-5 mm de terre humide à surface complètement lissée. Sur l'un des côtés, une lame couvre-objets a été légèrement surélévée de façon à permettre aux individus en élevage de s'y abriter. Ces boîtes ont ainsi été installées dans une chambre à 20-25°C pendant l'automne et l'hiver et à 22-26°C pendant le printemps et l'été. L'alimentation régulière des individus consistait en des larves de *Tenebrio molitor*, des petits grillons, des termites et des drosophiles ; de l'eau distillée était rajoutée afin de maintenir la terre humide. On remarque que, dans deux cas seulement, la femelle a dévoré le mâle et une seule fois le mâle a dévoré la femelle. En juin 1991, à l'exception d'un seul mâle isolé, tous les mâles étaient morts et il n'y avait donc plus aucun couple reproducteur. En ce qui concerne les femelles, seulement 8 sur 19 avaient survécu ; aucune observation en relation avec la reproduction n'avait été notée.

Le produit de la collecte de 1992 a été de 22♀, installées elles-aussi dans des conditions semblables. Toutefois, le premier substrat avait été changé, car suspecté d'avoir été la cause du taux élevé de mortalité. Le nouveau substrat utilisé a été obtenu par tamisage des premières couches du sol où les individus ont été récoltés, dans la Serra de Roqueroles.

Pendant la période de mai à août 1992, de nombreux oeufs fûrent comptabilisés, issus des pontes effectuées par 15 des 22 ♀ de 1992 et des 3 survivantes de 1990. Il faut cependant remarquer, concernant ces dernières, qu'on n'avait détecté aucun indice de l'existence d'une ponte en 1990 et en 1991. Etant donné qu'on n'a jamais observé de spermatophores, on peut en conclure que toutes les femelles se trouvaient dejà fécondées avant leur capture.

RÉSULTATS

Reproduction

Nos connaissances sur les différents aspects de la reproduction des espèces du genre *Lithobius*, telles que la formation des couples, l'émission des spermatophores, la fécondation, la taille des pontes, l'éclosion des oeufs, la survivance de chacun des stades larvaires, etc., sont très limitées. Peu de biologistes ont essayé de reproduire des espèces de *Lithobius* en captivité ; dans ce sens il faut remarquer le travail réalisé par DEMANGE (1956) sur *Lithobius piceus gracilitarsis*, qui apporte des données intéréssantes sur la biologie de cette espèce. ANDERSSON (1978a, 1981b) expose aussi brièvement la méthodologie utilisée pour réussir la reproduction de différentes espèces au laboratoire afin d'obtenir des exemplaires permettant l'étude du développement post-embryonnaire.

Le Tableau 1 donne le nombre d'oeufs pour la ponte de chacune des femelles, le nombre d'éclosions et le pourcentage de viabilité de celles-ci ainsi que les valeurs moyennes de ces paramètres.

L'énorme disparité de taille des pontes (entre 5 et 105 oeufs!) est difficilement explicable ; il faut tenir compte du fait que des oeufs ont pu échapper à notre attention car l'oothèque qui les protège est une petite boule de matériel du substrat. Il faut également remarquer que la diversité de taille des femelles indique que leur âge était sans doute différent. Dans tous les cas et avec ces conditions de reproduction en captivité, la valeur moyenne du pourcentage de viabilité des oeufs (m = 77,53%) est remarquablement élevée. Elle permet de supposer que, dans certaines populations sauvages elle pourrait être plus importante, ce qui indique un taux de reproduction assez élevé.

Source : MNHN, Paris

TABLEAU 1. — Dates de capture des différentes femelles ayant pondu, nombre d'oeufs, période de ponte, nombre d'éclosions et taux de survie à l'éclosion (%). $\overline{m}$ désigne les valeurs moyennes.

TABLE 1. — Catch dates of females showing egg deposition, number of eggs, egg-laying period, hatching, survival rate (%). $\overline{m}$ *= mean data.*

♀	Récolte	Oeufs	Ponte (1992)	Eclosion	%Viabilité
1	1.X.1990	30	Juillet	29	96,67
2	1.X.1990	24	Mai-Juillet	17	70,83
3	1.X.1990	26	Mai	23	88,46
4	6.IV.1992	45	Juin-Août	13	28,89
5	6.IV.1992	105	Juin-Août	65	61,90
6	6.IV.1992	105	Juin-Juillet	78	74,29
7	6.IV.1992	30	Juillet	21	70,00
8	6.IV.1992	6	Juillet	5	83,33
9	6.IV.1992	14	Juin-Juillet	6	42,86
10	6.IV.1992	41	Juin-Août	27	65,85
11	6.IV.1992	66	Juillet-Août	55	83,33
12	6.IV.1992	32	Juin-Juillet	31	96,87
13	6.IV.1992	6	Juin	6	100,00
14	6.IV.1992	7	Juillet	5	71,43
15	6.IV.1992	17	Juin-Juillet	16	94,12
16	6.IV.1992	45	Juin-Juillet	39	86,67
17	6.IV.1992	10	Juillet	8	80,00
18	6.IV.1992	5	Juin	5	100,00
		$\overline{m}$= 34,11		$\overline{m}$= 24,94	$\overline{m}$= 77,53

En diverses occasions, nous avons pu observer la ponte des oeufs par certaines femelles, ce qui nous a permis d'enregistrer ce processus sur une cassette-vidéo. Le mécanisme observé est très semblable à celui décrit par DEMANGE (1956). La femelle soutient l'oeuf avec les valves anales et les éperons gonopodiaux ; les gonopodes, très turgescents, donnent à l'œuf un mouvement de rotation en lui évitant tout contact avec le sol. Les ongles apicaux des gonopodes sont utilisées pour arracher les petites particules du sol et les coller à la surface de l'oeuf qui se trouve totalement imprégné d'une sécrétion visqueuse jusqu'à la formation de l'oothèque en forme de boule de boue. Cette dernière, sphérique, est remarquablement différente de celle de *Lithobius piceus gracilitarsis*, laquelle est de forme lenticulaire avec un gonflement au centre ; ce fait indique que la forme de l'oothèque est spécifique. La durée de la ponte varie entre une heure et demie et deux heures et se termine quand l'oothèque est abandonnée au sol.

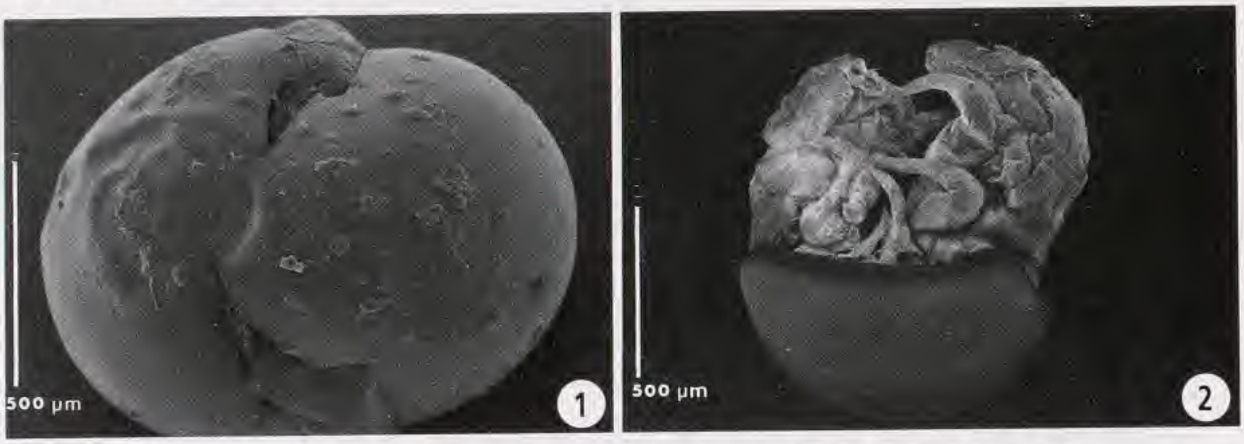
Nous avons isolé dans de petites boîtes munies du même substrat les oeufs qui viennent d'être pondus, ce qui a permis d'observer et d'enregistrer l'éclosion, au bout de 24 à 32 jours. Certains de ces oeufs ont été délicatement déshabillés de l'oothèque protectrice, ce qui a permis, par transparence, d'observer l'embryon, qui reste d'abord immobile et ne montre quelques mouvements qu'au moment de la naissance.

L'éclosion débute lorsque se produit la cassure des deux couches qui forment l'oeuf (Figs. 1 et 2), une couche externe plus épaisse et une autre interne plus fine, à travers une ligne medio-équatoriale. La tête est la première partie du corps qui sort de l'oeuf ; les antennes sont maintenues entre les forcipules de façon à rester dirigées vers l'arrière, repliées sur la partie ventrale du corps. Avec beaucoup d'efforts, la larve commence à extraire les premiers segments du corps, et dès que quelques-unes des premières paires de pattes sont libérées, le petit *Lithobius* les utilise pour libérer le reste du corps beaucoup plus rapidement. La nouvelle larve est très active dès qu'elle se sent libérée; cependant, dans aucun cas elle ne se nourrit, comme nous avons pu le constater. La durée du processus de la naissance : cassure de l'oeuf, jusqu'à l'abandon de celui-ci par la larve, est de 1,5 à 2 heures.

Au bout de deux ou trois jours, la larve subit une première mue, qui a été également enregistrée sur cassette-video. Le début du rejet de l'ancienne cuticule commence avec sa rupture

Source : MNHN, Paris

au niveau du sillon frontal de la région antéro-dorsale de la tête, immédiatement en arrière de celle-ci et ce sont les premiers articles des antennes qui apparaissent les premiers à l'extérieur. L'exuvie se replie progressivement jusqu'à la partie postérieure du corps et, simultanément, tout le corps sort de celle-ci ; l'extraction des antennes est sans doute la partie plus longue et la plus laborieuse du processus. A la fin de la mue, qui dure de 60 à 90 minutes, la nouvelle larve abandonne sa vieille cuticule ; elle y reviendra plus tard pour la dévorer. Il faut signaler qu'à partir du moment où la larve sort de sa vieille cuticule, elle passe beaucoup de temps à nettoyer ses antennes avec les maxilles et en s'aidant des forcipules pour les soutenir ; on remarque également que cette nouvelle larve est très active et qu'elle se nourrit de petits invertébrés tels que des enchytréides et des collemboles.



FIGS 1-2. — 1 : oeuf avec la ligne de cassure médio-équatoriale. 2 : larve sortant de l'oeuf.
FIGS 1-2. — 1: egg with medio-equatorial broken line. 2: hatching larva.

Le nombre de jours qui sépare deux mues successives, c'est-à-dire la durée de chacun des stades larvaires, est donnée ci-après ; la terminologie utilisée est celle d'ANDERSSON (1976, 1978a) :

Oeuf (24-32j.) → L0 (2-3j.) → LI (4-8j.) → LII (6-8j.) → LIII (39-44j.) → LIV (28-32j.) → PL

Description des larves

A partir des larves obtenues en captivité et dont l'âge est connu, on a pu étudier les variations des principales caractéristiques morphologiques de chacun des stades. Elles sont exposées dans le Tableau 2; les nombres entre parenthèse qui suivent le nombre de paires de pattes indique les paires de bourgeons pour chaque stade ; les valeurs de la longueur du corps d'une part, de la longueur et de la largeur de la tête d'autre part, sont exprimées en millimètres.

TABLEAU 2. — Principaux caractères morphologiques des stades larvaires (L0 à LIV) et du premier stade post-larvaire (PL).
TABLE 2. — Main morphological features of the larval stages (L0 to LIV) and the first post-larval stage (PL).

	L0	LI	LII	LIII	LIV	PL
Pattes	7	7(1)	8(2)	10(2)	12(3)	15
Tergites	8	8	9	11	13	15
Antennes	7+7	11+11	14+14	17+17	20+20	23-27
Ocelles	2	3	3	3	4-5	5-6-7
Cox. forcip.	-	2+2(3)	3+3	3+3	3+3	3+3
VmH	-	-	-	-	-	P.15
Long. corps	2,96-3,63	2,66-2,98	4,13-4,27	4,19-4,62	4,60-4,71	5,54
Long. tête	0,43-0,50	0,39-0,44	0,62-0,63	0,65-0,68	0,74-0,78	0,83
Larg. tête	0,58-0,68	0,50-0,52	0,62-0,65	0,67-0,74	0,74-0,76	0,82

Source : MNHN, Paris

Dans le Tableau 3 la spinulation des pattes est exposée pour chacun des stades larvaires. Pour chaque épine sont indiquées sa limite antérieure (première paire de pattes où elle apparaît) et sa limite postérieure (dernière paire de pattes qui la présente), séparées par un tiret. Dans le cas où l'une ou l'autre de ces limites varie selon les individus, les paires de pattes-limite (qu'elles soient antérieure ou postérieure), sont séparées par une virgule ; quand l'une de ces paires est plus fréquente, elle est indiquée en gras. Dans le premier stade post-larvaire, il y a une grande variabilité pour les limites de la majorité des épines, la plus variable étant la DmP qui se trouve en séries continues (7-12, 8-12, 8-14, 7-15, 8-15, 10-15) ou qui apparaît de façon irrégulière sur certaines pattes (6, 8, 10, 11, 12 ; 11, 12 ; 9, 10). On remarque aussi que l'épine VmH, caractéristique de *Lithobius pilicornis,* apparaît au stade post-larvaire (PL), le premier stade où l'on trouve la paire de pattes 15, chez tous les exemplaires.

TABLEAU 3. — Spinulations des stades larvaires (LO à LIV) et du premier stade post-larvaire (PL).
TABLE 3. — Diagram of spinulation of the larval stages (L0 to LIV) and the first post-larval stage (PL).

	L0	LI	LII	LIII	LIV	PL
DmP	-	-	-	-	8-10	6 . . . 15
DpP	-	-	-	-	**4**,6,7,8-10	**2**,3,6-9,**12**,15
DaF	1-3,**4**,5	1-7	1-8	**1**,4-8 -	2,5,**6**,7-**8**,10,11	1,2,3,5-10,11,12,13
DpF	-	-	-	-	7,8,**9**-10	2,3,4,5-12,14,15
DaT	1-7	**1**,5-7	1-8	1-9,**10**	**1**,2,3,5-7,8,9,**10**	1,2,4-10,11,**12**
DpT	-	-	-	-	-	6,7,8,9,-12,13,14
VmH	-	-	-	-	-	15
Vmtr	-	-	-	-	-	**13**,15
VaP	-	-	-	-	-	**15**/13-15
VmP	-	-	-	1,4,8-10	**1**,2-12	1-15
VpP	-	-	-	-	-	**12**,14-15
VaF	-	-	-	-	-	4,5,6,**8**,9-12,14,**15**
VmF	**1**,2-7	**1**,2-7	1-8	**1**,5-10	1-12	1-15
VmT	1-7	1-7	1-8	1-10	1-12	1-13,**14**,15

RÉFÉRENCES

ANDERSSON, G., 1976. — Post-embryonic development of *Lithobius forficatus* (L.), (Chilopoda: Lithobiidae). *Ent. scand.*, **7** : 161-168.

ANDERSSON, G., 1978a. — An Investigation of the Post-Embryonic Development of the Lithobiidae. Some Introductory Aspects. *Abh. Verh. naturwiss. Ver. Hamburg, (NF)* , **21/22** : 63-71.

ANDERSSON, G., 1978b. — Post-embryonic development of *Lithobius erythrocephalus* C. L. Koch (Chilopoda: Lithobiidae). *Ent. scand.*, **9** : 241-246.

ANDERSSON, G., 1979. — On the use of larval characters in the classification of Lithobiomorph Centipedes (Chilopoda, Lihobiomorpha). *In* : M. CAMATINI, *Myriapod Biology*. London, Academic Press : 73-81.

ANDERSSON, G., 1980. — Post-embryonic development of *Lithobius melanops* Newport (Chilopoda: Lithobiidae). *Ent. scand.*, **11** : 225-230.

ANDERSSON, G., 1981a. — Post-embryonic development and geographical variation in Sweden of *Lithobius crassipes* L. Koch (Chilopoda: Lithobiidae). *Ent. scand.*, **12** : 437-445.

ANDERSSON, G., 1981b. — Taxonomical studies on the post-embryonic in Swedish Lithobiomorpha (Chilopoda). *Ent. scand.*, **Suppl. 16** : 105-124.

ANDERSSON, G., 1982a. — Post-embryonic development of *Lithobius calcaratus* C. L. Koch (Chilopoda: Lithobiidae). *Ent. scand.*, **13** : 435-440.

ANDERSSON, G., 1982b. — Post-embryonic development of *Lithobius microps* Meinert (Chilopoda: Lithobiidae). *Ent. scand.*, **13** : 89-95.

ANDERSSON, G., 1983. — Post-embryonic development of *Lithobius curtipes* C. L. Koch (Chilopoda: Lithobiidae). *Ent. scand.*, **14** : 387-394.

ANDERSSON, G., 1984a. — Post-embryonic development of *Lithobius tenebrosus fennoscandius* Lohmander (Chilopoda: Lithobiidae). *Ent. scand.*, **15** : 1-7.

Source : MNHN, Paris

ANDERSSON, G., 1984b. — Post-embryonic development of *Lamyctes fulvicornis* Meinert (Chilopoda: Henicopidae). *Ent. scand.*, **15** : 9-14.

ANDERSSON, G., 1990. — About the duration of the different stadia in the post-embryonic development of some Lithobiomorph species. *In* : A. MINELLI, *Proceedings 7th Intern. Congr. Myriapodology*. Leiden, Brill : 323-335.

BROLEMANN, H. W., 1930. — *Éléments d'une Faune des Myriapodes de France. Chilopodes*. [*Faune Fr.*, **25**], Paris, P. Lechevalier : 1-405.

DEMANGE, J. M., 1956. — Contribution à l'étude de la biologie, en captivité, de *Lithobius piceus gracilitarsis* Bröl. (Myriapode-Chilopode). *Bull. Mus. natl. Hist. nat., 2e sér.*, **28** : 388-393.

EASON, E. H., 1964. — *Centipedes of the British Isles*. London, F. Warne & Co Ltd, 294 pp.

EASON, E. H., 1970. — The Chilopoda and Diplopoda of Iceland. *Ent. Scand.*, **1** : 47-54.

MURAKAMI, Y., 1958. — The life-history of *Bothropolys asperatus* (L. Koch). *Zool. Mag. Tokyo*, **67** : 217-223.

MURAKAMI, Y., 1960. — Postembryonic development of the common Myriapoda of Japan. V: *Lithobius pachypedatus* Takakuwa (Chilopoda, Lithobiidae). 3. Variation in the number of articles of antennae and coxal pores. *Zool. Mag. Tokyo*, **69** : 167-170.

SCHEFFEL, 1969. — Untersuchungen über die hormonale Regulation von Häutung und Anamorphose von *Lithobius forficatus* L. (Myriapoda, Chilopoda). *Zool. Jb. Physiol.*, **74** : 436-505.

VERHOEFF, K. W., 1905. — Über die Entwicklungsstufen der Steinläufer, Lithobiiden, und Beiträge zur Kenntnis der Chilopoden. *Zool. Jb.*, **Suppl. 8** : 195-298.

Source : MNHN, Paris

Développement post-embryonnaire et cycle biologique de *Eupolybothrus elongatus* (Newport) dans l'est algérien

Tarek* DAAS *, *Noureddine* BOUZERNA * & *Michel* DESCAMPS *

* Institut des Sciences de la Nature, Laboratoire de Biologie Animale
Université de Annaba, BP 12 Annaba, Algérie

** Ecophysiologie d'Invertébrés du Sol, Laboratoire de Biologie Animale, Université de Lille I
F-59655 Villeneuve d'Ascq Cedex, France
(to whom all correspondence must be sent)

RÉSUMÉ

Le cycle de développement du Chilopode *Eupolybothrus elongatus* a été suivi dans la région d'Annaba, à l'Est de l'Algérie. Les caractéristiques des différents stades ont été décrites (nombre de paires de pattes, de segments antennaires, longueur et, pour les stades épimorphes, masse moyenne). L'abondance relative des différents stades a été évaluée en utilisant des pièges. Les observations sur le terrain, sur deux sites à couverture végétale différente (Sidi Amar : forêt d'*Eucalyptus* ; Oued Zied : steppe de type méditerranéen), ont permis de reconnaître deux périodes de ponte préférentielles, d'octobre à janvier, et, dans une moindre mesure, d'avril à juin-juillet. Le travail, mené en parallèle sur les deux zones d'étude, a permis de mettre en évidence l'influence du milieu. Les résultats montrent l'importance des facteurs externes sur le taux de capture : les mois les plus secs sont caractérisés par l'absence (ou la quasi-absence) d'adultes dans les pièges, même dans le biotope le moins aride.

ABSTRACT

Post-embryonic development and life-cycle of *Eupolybothrus elongatus* (Newport) in Eastern Algeria.

The biological cycle of the chilopod *Eupolybothrus elongatus* has been studied in Eastern Algeria, near Annaba. The characteristics of the different stages are described (number of leg pairs and of antennal segments, length of animal and, for the epimorphic stages, mean mass). The relative abundance in the field of the different stages has been estimated by using pitfall traps. The results concerning two sample sites with different kinds of vegetation (Sidi Amar: *Eucalyptus* forest; Oued Zied: Mediterranean steppe) show two egg-laying periods, from October to January, and at a lesser extend, from April to June-July. Analysis of the results from the two sample sites points out the influence of rainy periods: the driest months are characterized by no adults (or so) in traps, even for the less arid biotope.

DAAS, T., BOUZERNA, N. & DESCAMPS, M., 1996. — Développement post-embryonnaire et cycle biologique de *Eupolybothrus elongatus* (Newport) dans l'est algérien. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 365-370. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

INTRODUCTION

Chez les chilopodes, la plupart des recherches en physiologie expérimentale ont été menées chez *Lithobius forficatus* (L.) (cf. les mises au point de SCHEFFEL, 1987 ; JOLY & DESCAMPS, 1988 ; DESCAMPS, 1992). Seuls quelques travaux ont été menés sur d'autres espèces (*Scolopendra cingulata* : JOLY, 1966 ; *L. crassipes* : BENIOURI *et al.*, 1983).

En ce qui concerne le cycle biologique, la succession des stades et la croissance ont été bien étudiées chez différents *Lithobius*, en particulier, pour citer les travaux les plus récents, par ANDERSSON (1976-1984). Le genre "*Bothropolys*" n'a été étudié que par MURAKAMI (*B. asperatus*, 1958). Le chilopode le plus commun dans la région d'Annaba est *Eupolybothrus elongatus* (Newport, 1849), ex-*Bothropolys elongatus* auct. (cf. EASON, 1972 ; MATIC, 1974). Avant d'entreprendre une étude expérimentale sur ce matériel, il nous est apparu nécessaire d'en connaître le cycle biologique dans son environnement méditerranéen.

MATÉRIEL ET MÉTHODES

Elevage au laboratoire

Les animaux, récoltés dans divers biotopes autour d'Annaba, sont maintenus dans des boîtes en plastique où se trouve de la terre humidifiée recouverte d'un papier filtre imbibé d'eau. Les animaux sont nourris régulièrement avec des moustiques, des mouches ou de petites araignées. La température d'élevage a varié en cours d'année entre 10°C (janvier) et 26,5°C (août), reflètant en cela les variations de température externe (de 10°C à 29,2°C).

Des pontes ont été obtenues au laboratoire, qui nous ont permis d'étudier les caractéristiques des premiers stades larvaires. Les stades les plus âgés ont été suivis à partir d'animaux récoltés dans la nature. Les résultats exprimés dans les tableaux correspondent à un minimum de 4 observations.

Récoltes sur le terrain

Deux stations ont été étudiées : Sidi Amar (forêt d'*Eucalyptus*) et Oued Zied (steppe de type méditerranéen). Les pièges d'interception (pitfall trap), garnis d'eau formolée, sont relevés au bout de 4 jours. Quatre prélèvements par mois ont été faits au cours de la période d'étude (novembre 1990 - octobre 1991).

RÉSULTATS

Développement post-embryonnaire

Nous avons pu reconnaître 5 stades larvaires (L0 à L4 suivant la nomenclature de ANDERSSON, 1978), dont les durées de développement sont consignées dans le Tableau 1 et les caractéristiques dans le Tableau 2. A partir du stade PL4, les durées d'intermue deviennent très longues (45 jours et plus).

TABLEAU 1. — Durée des stades, de la ponte à la larve 4, chez *E. elongatus* (d'après des observations faites entre octobre 1990 et mai 1991).

TABLE 1. — Post-embryonic stadia of E. elongatus, *duration in days, from egg to post-larval stage 4 (after observations made between October, 1990 and May, 1991).*

Stades	Durée (en jours)
oeuf	21 à 25
Larve 0	13 à 22
Larve 1	3
Larve 2	10
Larve 3	10 à 13
Larve 4	19
Post-larve 1	13 à 17
Post-larve 2	33
Post-larve 3	30 à 36
Post-larve 4	45

Source : MNHN, Paris

TABLEAU 2. — Caractéristiques des stades larvaires et post-larvaires chez *E. elongatus*.
TABLE 2. — Morphological features of larval and post-larval stages of E. elongatus.

Stades	Nb. de paires de pattes	Nb. d'articles antennaires	Longueur (mm)	Masse (mg)	
Larve 0	7	9	5 à 6		
Larve 1	8	11 à 13	6,5		
Larve 2	9	15	7		
Larve 3	11	17	7,5		
Larve 4	13 à 14	21	8		
PL 1	15	34 à 36	9 à 11	4,1 à 6,3	
PL 2	15	38	13 à 15	11,5 à 20	
PL 3	15	38 à 39	16 à 18	23,5 à 40	
PL 4	15	39 à 40	19	45 à 62	52 à 75
PL 5	15	40	21 à 23	75 à 85	80 à 115
PL 6	15	41 à 42	27 à 30	93 à 140	120 à 165
> à PL 6	15	42 à 43	33 à 45	156 à 200	180 à 260
				femelles	mâles

Cycle biologique

Les résultats des récoltes sont consignés dans les Tableaux 3 (Sidi Amar) et 4 (Oued Zied). En ce qui concerne Sidi Amar, nous pouvons constater un maximum de stades larvaires piégés au cours du mois de décembre. Compte tenu de la durée de l'incubation et des stades larvaires obtenus au laboratoire, nous pouvons dire que les pontes ont lieu préférentiellement entre octobre et janvier. Une autre période de ponte, moins favorable semble-t-il d'après le nombre de captures, intervient entre avril et juin-juillet. Le maximum de capture des stades post-larvaires est lui, atteint au mois de janvier. Notons un minimum dans les récoltes d'adultes (PL6 et au-dessus) en août et septembre.

Le site de Oued Zied est beaucoup plus pauvre en faune, mais on peut observer à peu près les mêmes phénomènes qu'à Sidi Amar, avec cependant une période d'absence de grands stades post-larvaires durant la période mai-août (plus octobre).

DISCUSSION ET CONCLUSION

Le premier point que nous voudrions discuter concerne les caractéristiques du stade L0 : la durée de ce stade au laboratoire nous a semblé anormalement longue. En effet, les différents travaux faisant état de la durée des premiers stades larvaires indiquent que ceux-ci n'excèdent jamais quelques jours (1 à 3 en général). Nos observations ont porté sur 9 individus, issus d'une ponte de 15 oeufs. Si les caractéristiques morphologiques permettent de séparer nettement les stades L0 et L1, il n'en reste pas moins étonnant qu'il y ait une aussi grande différence de durée entre ces deux stades successifs. Il est donc possible que nous ayons observé, par une malheureuse coïncidence, des larves au développement perturbé par une cause inconnue. La réponse ne pourra bien sûr être apportée qu'en étudiant un plus grand nombre d'individus provenant de femelles prélevées dans différents lieux de récolte.

En ce qui concernant les autres stades, nous sommes en présence du développement classique d'un chilopode lithobiomorphe.

Source : MNHN, Paris

TABLEAU 3. — Récoltes sur le site de Sidi Amar.
TABLE 3. — Number of individuals collected at Sidi Amar.

	Nov.	Déc.	Jan.	Fév.	Mars	Avr.	Mai	Juin	Juil.	Août	Sept.	Oct.
Larve 1		1										
Larve 2	3	3	2									
Larve 3	1	2	1						1	1		
Larve 4	1	5	2	2	4		1			1	1	1
PL 1			4						1			
PL 2	4	6	5	4	2	2	3	1	5	2	4	3
PL 3	2	3	11	5	3	2		2		4	3	5
PL 4 & 5	5	5	9	3	5	7	5	1	3	6	5	4
PL 6	3	9	11	8	8	5	3	4	2	3		2
> à PL 6	4	3	4	3	2		1	1	3			2
Total larves	5	11	5	2	4	0	1	0	1	2	1	1
Total PL 1 à PL 5	11	14	29	12	10	11	8	4	9	12	12	12
Total matures (> PL 5)	7	12	15	11	10	5	4	5	5	3	0	4
Total général	23	37	49	25	24	16	13	9	15	17	13	17

TABLEAU 4. — Récoltes sur le site de Oued Zied.
TABLE 4. — Number of individuals collected at Oued Zied.

	Nov.	Déc.	Jan.	Fév.	Mars	Avr.	Mai	Juin	Juil.	Août	Sept.	Oct.
Larve 1												
Larve 2												
Larve 3												
Larve 4		1		1							1	
PL 1	1										1	2
PL 2					4					3	1	
PL 3	5	2	4	2	5	1					3	3
PL 4 & 5	4	3	5	4	1	3				5	2	4
PL 6	3	2	2	3	3	1					2	
> à PL 6			1								1	
Total larves	0	1	0	1	0	0	0	0	0	0	1	0
Total PL 1 à PL 5	10	5	9	6	10	4	0	0	0	8	7	9
Total matures (> à PL 5)	3	2	3	3	3	1	0	0	0	0	3	0
Total général	13	8	12	10	13	5	0	0	0	8	11	9

Source : MNHN, Paris

Le second point de discussion concerne la méthodologie utilisée lors des récoltes : en effet, le piégeage d'interception (pitfall trap) est peu propice à la récolte des stades jeunes (voir les articles de BRANQUART & GASPAR et de GEOFFROY & CÉLÉRIER dans ce volume) ; néanmoins, s'agissant de l'étude d'une seule et même population spécifique, et notre but étant la recherche du déroulement d'un cycle et non l'estimation correcte d'une densité de population, les résultats restent significatifs.

Enfin, ce qui nous semble important au point de vue du cycle biologique, est pour le site de Oued Zied, l'absence ou la quasi absence d'individus dont les caractéristiques morphologiques correspondraient à des stades postérieurs à PL6. Comme il est statistiquement improbable que nous n'ayons récolté que de jeunes individus, il nous faut plutôt conclure à une population de taille moyenne plus faible, en rapport avec une nourriture disponible plus faible (aridité du milieu).

Le rythme saisonnier, caractérisé par l'absence de grands froids, par des périodes de grande chaleur (juillet et août), par la sécheresse, peut expliquer, avec un décalage dans le temps que l'on pourrait qualifier d'"inertie du système", l'absence ou la diminution de l'activité-densité des populations durant les périodes les plus chaudes et les plus arides. Inversement, c'est durant les périodes les plus humides que l'on obtient les maximums de récolte.

Les populations de *E. elongatus* sont donc fortement inféodées aux conditions climatiques, et l'on peut d'ores et déjà conclure que comme *L. forficatus* (DESCAMPS, 1971 ; HERBAUT, 1975), cet animal possède une physiologie qui est fortement sous la dépendance des facteurs externes, en particulier de la température.

REFERENCES

ANDERSSON, G., 1976. — Post-embryonic development of *Lithobius forficatus* (L.), (Chilopoda : Lithobiidae). *Ent. scand.*, **7** : 161-168.

ANDERSSON, G., 1978. — An investigation of the post-embryonic development of the Lithobiidae - Some introductory aspects. *Abh. Verh. naturwiss. Ver. Hamburg* , **21/22** : 63-71.

ANDERSSON, G., 1981. — Post-embryonic development and geographical variation in Sweden of *Lithobius crassipes* L. Koch (Chilopoda : Lithobiidae). *Ent. scand.*, **12** : 437-445.

ANDERSSON, G., 1982. — Post-embryonic development of *Lithobius microps* Meinert (Chilopoda : Lithobiidae). *Ent. scand.*, **13** : 89-95.

ANDERSSON, G., 1983. — Post-embryonic development of *Lithobius curtipes* C. L. Koch (Chilopoda : Lithobiidae). *Ent. scand.*, **14** : 387-394.

ANDERSSON, G., 1984. — Post-embryonic development of *Lithobius tenebrosus fennoscandius* Lohmander (Chilopoda : Lithobiidae). *Ent. scand.*, **15** : 1-7.

BENIOURI, R., DESCAMPS, M., PORCHERON, P. & JOLY, R., 1983. — Corrélations naturelles et expérimentales entre croissance spermatocytaire et taux d'ecdystéroïdes chez les Lithobiidae (Chilopoda). *Rev. Can. Biol. Experiment.*, **42** : 183-189.

BRANQUART, E. & GASPAR, C., in press. — Comparative study of sampling techniques of saprophagous macroarthropods (Diplopoda and Isopoda).

DESCAMPS, M., 1971. — Le cycle spermatogénétique chez *Lithobius forficatus* (L.) (Myriapode, Chilopode). II. Influence des facteurs externes sur l'évolution du testicule et des vésicules séminales. *Arch. Zool. exp. gén.*, **112** : 731-746.

DESCAMPS, M., 1992. — Endocrine events during the life cycle of *Lithobius forficatus* (L.). *Ber. nat.-med. Verein Innsbruck* , **suppl 10** : 11-116.

EASON, E. A., 1972. — The type specimens and identity of the species described in the genus *Lithobius* by George Newport in 1844, 1845 and 1849. *Bull. Br. Mus. nat. Hist. (Zool.)*, **21** : 297-311.

HERBAUT, C., 1975. — Influence des facteurs externes sur le cycle ovogénétique chez *Lithobius forficatus* (L.) (Myriapode Chilopode). *Arch. Zool. exp. gén.*, **116** : 293-302.

JOLY, R., 1966. — Contribution à l'étude du cycle de mue et de son déterminisme chez les Myriapodes Chilopodes. *Bull. Biol. Fr. Belg.*, **3** : 379-480.

JOLY, R., DESCAMPS, M., 1988. — Endocrinology of Myriapods. *In* : H. LAUFER & R. G. H. DOWNER, *Endocrinology of Selected Invertebrate Types* . New York, Alan R. Liss : 429-449.

Source : MNHN, Paris

MATIC, Z., 1974. — Contribution à la connaissance du genre *Bothropolys* Wood, 1863 (Lithobiomorpha, Ethopolidae). *Ann. Zool., Warsawa*, **31** : 329-341.

MURAKAMI, Y., 1958. — The life-history of *Bothropolys asperatus* (L. Koch). *Zool. Mag. Tokyo*, **67** : 217-223.

SCHEFFEL, H., 1987. — Häutungsphysiologie der Chilopoden : Ergebnisse von Untersuchungen am *Lithobius forficatus* (L.). *Zool. Jb. Physiol.*, **91** : 257-282.

Source : MNHN, Paris

The Segmentation of the Head and Anterior Trunk of Millipedes (Diplopoda) - A Reassessment

Wolfgang DOHLE

Institut für Zoologie, Königin-Luise-Str. 1-3, D-1000 Berlin, 33, Germany

ABSTRACT

In recent years, the segmentation of the head and trunk of arthropods has gained new interest through the revelation and characterization of segment polarity genes and pair rule genes. Are there indications of a general double-segment organization in millipedes? A reinvestigation of germ band formation in the millipede *Glomeris marginata* was performed with fluorescent dyes and with SEM. Most results which had been gained by traditional histological methods have been confirmed. The intercalary segment remains without appendage buds. The mandibles become subdivided into 2 articles. The gnathochilarium is formed by the first maxillae and the triangular sternite of this segment. There is no indication of appendage buds on the postmaxillary segment. The first 4 trunk segments are simple segments with one pair of groove-like invaginations for the formation of the ganglia. Only in the subsequent segments (V+VI, VII+VIII) the lateral and dorsal parts combine to form double-pleurites and double-tergites.

RÉSUMÉ

La segmentation de la tête et de la partie antérieure du tronc chez les diplopodes - une réévaluation.

Durant ces dernières années, l'étude de la segmentation de la tête et du tronc des Arthropodes a connu un regain d'intérêt grâce à la découverte et à la caractérisation de gènes gouvernant la polarité de la segmentation et déterminant l'association des segments par paires. Y-a-t-il alors des informations relatives à une organisation générale d'une double segmentation chez les diplopodes? Une réévaluation de la formation de la bande germinale chez le diplopode *Glomeris marginata* a été effectuée dans ce but à l'aide de coloration en fluorescence et en microscopie électronique à balayage (MEB). La plupart des résultats qui avaient été acquis grâce aux techniques histologiques traditionnelles ont été confirmés. Le segment intercalaire demeure dépourvu de bourgeons. Les mandibules commencent à se subdiviser en deux articles. Le gnathochilarium est formé par la première paire de maxilles et le sternite triangulaire correspondant. Nous n'avons aucune confirmation concernant la présence de bourgeons appendiculaires sur le segment post-maxillaire. Les quatre premiers segments du tronc sont simples et présentent une paire d'invaginations en forme de rainure qui conduisent à la formation de ganglions. Ce n'est que dans les segments suivants (V+VI, VII+VIII) que les parties latérales et dorsales se combinent pour former des double-pleurites et des double-tergites.

DOHLE, W., 1996. — The segmentation of the head and anterior trunk of millipedes (Diplopoda) - A reassessment. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 371. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

Source : MNHN, Paris

On Periodomorphosis, Iteroparity and Life-Cycles in Males and Females of *Tachypodoiulus niger* (Leach) (Myriapoda, Diplopoda, Julidae) in France, Germany and Great-Britain

François SAHLI

Muséum National d'Histoire Naturelle, Zoologie/Arthropodes, 61 rue Buffon, F-75231 Paris Cedex 05
& Laboratoire souterrain du CNRS, F-09200 Moulis, France

ABSTRACT

In spite of appearances, the cycles and life-history of *Tachypodoiulus niger* have been hitherto poorly known. In the same way as he did previously in *Ommatoiulus sabulosus*, the author describes and interprets the cycles of *Tachypodoiulus niger*, particularly according to VERHOEFF's investigations in Germany, those of FAIRHURST in Great-Britain, and to the author's 38 years of mostly unpublished data and experiments on this species in France, Germany and Great-Britain, and in the light of recent knowledge.

RÉSUMÉ

Sur la périodomorphose, l'itéroparité et les cycles de vie des mâles et des femelles de *Tachypodoiulus niger* (Leach) (*Myriapoda, Diplopoda, Julidae*) en France, Allemagne et Grande-Bretagne.

En dépit des apparences, les cycles de *Tachypodoiulus niger* sont mal connus. Comme il l'a fait antérieurement pour *Ommatoiulus sabulosus*, l'auteur décrit et interprète les cycles de *Tachypodoiulus niger*. Pour ce faire, il s'appuie sur les investigations de VERHOEFF en Allemagne, de FAIRHURST en Grande-Bretagne, ainsi que sur des données et expériences - pour la plupart inédites - de 38 années de recherches personnelles sur cette espèce en France, en Allemagne et en Grande-Bretagne. Les interprétations ont, de plus, été faites à la lumière de nos connaissances actuelles sur la périodomorphose.

INTRODUCTION

Our current knowledge of the cycles in *T. niger* mainly goes back to the data of VERHOEFF (1915-1934: particularly 1928, 1932) and SAHLI (1966). In collaboration with J. G. BLOWER, FAIRHURST (1968) translated the data of his predecessors into English, mentionned those of HALKKA (1958) and added his own worthwhile observations.

[In reading SAHLI's thesis (1966) the British authors did not understand that in *Tachypodoiulus* (and *Ommatoiulus*) it is possible for a specialist - taking attention to details - to distinguish an intercalary from a juvenile male (cf. SAHLI, 1966): only *extremely rare* cases (say in the region of 1: 500 intercalaries) may constitute exceptions].

SAHLI, F., 1996. — On periodomorphosis, iteroparity and life-cycles in males and females of *Tachypodoiulus niger* (Leach) (Myriapoda, Diplopoda, Julidae) in France, Germany and Great-Britain. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 373-384. Paris
ISBN : 2-85653-502-X.

Source : MNHN, Paris

New investigations were made by the present author from 1966 to 1992, in Burgundy, the French Pyrenees (Ariège), French Alps, Germany and Great Britain. On the one side, these researches and on the other the reinterpretation of VERHOEFF's data and my own prior to 1966, showed that the cycles of *T. niger* were still poorly understood and much more complicated than myriapdologists thought.

[Concerning cycles, periodomorphosis, adult to adult moults and combined strategies, HOPKIN & READ (1992) partly overlook or misinterpret some recent results of the present author, concerning, among others, *Tachypodoiulus* sp., *Ommatoiulus* sp., *Allajulus nitidus* and *Blaniulus guttulatus*].

This paper aims to set the record straight regarding our knowledge of cycles in *Tachypodoiulus niger*.

ADOPTED NOMENCLATURE

The definitions and abbreviations used here have been given in several previous papers (SAHLI 1990a, b, 1991a, b, c) to which the reader is referred.

Concerning the seriations, from reasons of symmetry, and taking into account the intercalary appearance season, the same numbers as those adopted for *O. sabulosus* (i.e. seriation 1: intercalaries s1 in autumn of the year x; seriation 2: intercalaries s1 in spring of the year x+1) will be used for *T. niger* (Table 3). We will add a seriation 3 and 3' specific to *Tachypodoiulus*.

RESULTS

My own cultures, experimental investigations, field observations, along with those of VERHOEFF (*passim*) led to the results recorded in Tables 1-8 and in Figures 1 and 2.

At low altitudes, ad1 production (maturation moults of juvenile to first adult males ad1 = MMJ) can take place (see, among others, Table 7) in the following ways:

- (case a) at the end of the winter/spring of the year x (before mating and egg deposition),
- (case b) at the summer/autumn of the year x (i.e. several months before egg-laying in spring of the year x+1, as it is the case in *Allajulus nitidus*). Nevertheless, mating can additionally take place in autumn of the year x,
- both cases (a and b) in the same year.

In other words, depending on the environmental conditions, *T. niger* is able to use two strategies of ad1 male production (either spring or autumn), or a combination of the two (spring + autumn).

Results concerning seasonal cycles in *T. niger* are recorded in Table 4. This gives the "base cycle" which includes *all fundamental possibilities*. From the 8 basic possibilities (a to h) one can derive all the possible ways, should one wish to go into details and individual cases. From the base cycle all the possible patterns can be reconstituted.

Base cycles have been given for *O. sabulosus* in Burgundy (SAHLI, 1990a , Fig.1) and for Mediterranean populations (SAHLI, 1991a, b, Table 1). [In Sahli (1991, table 1) a forgotten vertical line should connect the ad1 (in case b, seriation 1''β) and the s1 (in case a, seriation 1β) in summer. In the same table, the two vertical unbroken lines must be regarded as two vertical braces].

INTERPRETATION AND DISCUSSION

As in *O. sabulosus*, short standing (SL) and long-standing (LL) intercalaries exist in *T. niger* (SAHLI, 1990b).

Results taking into account the author's experimental data and field observations, as well as VERHOEFF's investigations are recorded in Tables 1 & 2. In the present state of our knowledge, two cases can be distinguished in Germany and Burgundy up to 1000 m altitude: one in lowlands and hills, another in the Allgau mountains (800 m) and in a rock shelter in the Saarland, both in Germany.

As shown in Tables 1 & 2, in the sites under 1000 m, there are two typical possibilities, at least in the present state of our knowledge:

Source : MNHN, Paris

TABLE 1. — The two possible cases in *T. niger*, at an altitude under 1050 m in some German regions (particularly in Saarland) and in Burgundy. SUM = summer.

Case a	SPRING		SUM-AUTUMN
Egg deposition	+		
ad1 production	+	and/or	+
sch ♂ production (ad-sch♂)			+
ad2 production (sch♂-ad2)			
- ad2 of SL origin	few		
- ad2 of LL origin			+
Case b	SPRING		SUM-AUTUMN
egg deposition			+ (?)
typical ad1 poduction			+
typical sch♂ production	+		

TABLE 2. — *T. niger* in Burgundy and some German regions. A: subdivision of ad1. B: typical appearance of sch ♂. In case b', ad1 mating is also possible -(first-) in autumn of year x.

A	Spring	Sum/Autumn
case a : spring ad1 (reproduction = year x)	+	
case b : summer/autumn ad1 (= reproduction year x)		+
case b' : summer/autumn ad1 (= main reproduction year x+1)		+
B	Spring	Sum/Autumn
case a : sch♂ from ad1 of case a		+
case b : sch♂ from ad1 of case b	+	

- *case a* = in Burgundy (at the numerous sites studied) and in epigean animals from Germany (Saarland, Hunsrück, Eifel, Rheinland, Taunus and Hessen). In this case: (a1) egg laying takes place in spring; (a2) ad1 production in spring and/or autumn; (a3) typical - or majority - sch♂ production in summer/autumn. Sch♂ are mainly (or only?) made up of LL and R individuals. The predominance of LL in *T. niger* contrasts with that of SL in Mediterranean *O. sabulosus* and probably in *O. moreleti* in Australia and southern Portugal (BAKER, 1978, 1984).

- *case b* = in Germany in the Allgau (750-1050 m), at least according to the culture results of VERHOEFF (1934), and in a rock shelter at Wadern in Saarland. In this case : (b1) egg laying(?) and ad1 male production take place at the end of summer/onset of autumn; (b2) sch♂ are produced in spring. In VERHOEFF's cultures (from 1924 to 1928) only sch♂ SL (thus an α succession) were observed. (The question of whether this was the result of the culture conditions remains open). A complete absence of LL sch♂ in the Allgau mountains would be astonishing. In Saar cultures (in a unheated basement - with open windows - of the Saarland University) of individuals collected in the Wadern rock shelter, the following succession has been observed: ad (collected in autumn x) - s (spring x+1) - ss (autumn x+1). A succession β (with R sch♂) as been obtained instead of the α one (ad—s—ad) of VERHOEFF.

In case a, some sch♂ (ad-sch♂) may sometimes be (exceptionally?) produced in spring in Burgundy, as well as in Saarland. If this occur, such sch♂ (which would be SL ones) could be regarded as minority sch♂ in comparison with the whole sch♂ liable to be collected in spring.

Like his predecessors, FAIRHURST(1968, 1974) was unaware of the existence of LL sch♂. He also did not know about the possibility for adults maturing in autumn to stay adults without moulting until the following spring. He trusted the informations given by VERHOEFF

Source : MNHN, Paris

(*passim*) and HALKKA (1958). For these reasons, it seems that FAIRHURST regarded - at least implicitly - the spring postadult male production (e.g. the passage from males become SL intercalaries 1 in autumn into ad2 males in the following spring) as common, even exclusive (based on the last row of ocelli appeared in animals preserved in alcohol). In the same way, FAIRHURST regarded implicitly the ad-sch♂ moult as common in spring (sch♂ being produced in spring from adults which become adults in the previous autumn).

TABLE 3. — Numeration adopted for the seriations in Burgundy and some regions of Germany. Seriations 1 and 2 - homologous to those 1 and 2 of *T. niger* - exist in *O. sabulosus*.

spring (year x) ad1 ♂♂ (low altitudes: Burgundy, Germany) SERIATION 1: s1 intercalaries in summer/autumn (year x) (cf *O. sabulosus*)
summer (year x) ad1 ♂♂ (e.g. in the Allgau mountains) reproduction period = year x SERIATION 2: s1 intercalaries in spring x+1
summer/autumn ad1 ♂♂ (year x) (in Germany plains) typical reproduction period = year x+1 SERIATIONS 3 & 3': s1 intercalaries = at the end of spring or sum/autum year x+1

TABLE 4. — Basic cycle of *T. niger* in Burgundy, Great-Britain and some German regions. **A**: starting from ad1, becoming adults in spring (SP). **B** and **C**: starting from ad1, becoming adults in summer (SUM) /autumn (AUT). SER.: seriation. Unbroken line means a moult. Dotted line means no moult.

CASE	SER	SP x	SUM-AUT x	SP x+1	SUM-AUT x+1
A					
a	1 SL	ad1 ———	s1 ———	ad2	
b	1 LL α			↗ ———	ad2
		ad1 ———	s1	s1	
c	1 LL β			↘ ———	ss
B					
d	2 SL α		ad1 ———	s1 ———	ad1
e	2 LL β		ad1 ———	s1 ———	ss
C					
f	3α		ad1	ad1 ——— s1 ———	ad2
g	3β		ad1	ad1 ——— s1 ———	ss
h	3'		ad1	ad1 .... ad1 ———	? s1

In the present state of our knowledge in Burgundy and in Germany, SL successions never appear as exclusive or even common. From numerous cultured animals in different conditions and during several years, I never obtained spring intercalaries from epigeous adult males (say ad1 or presumed ad2) collected in the previous autumn. I obtained spring intercalaries only from adults collected in the rock shelter at Wadern in autumn (case b). Conversely, sch♂ collected in autumn, as well as as sch♂ (particularly s1 ones) obtained in cultures in summer/autumn, never gave postimaginal adults the following spring in cultures. Only autumn sch♂ from the Wadern's rock shelter gave spring postadult males (case b).

It is possible that spring SL (case b) exist in a more or less high numbers in Great-Britain. Nevertheless, according to my own investigations made at Milldale (G.B.) in 1981 and 1983, the cycle seems to include fundamentally sch♂ LL (case a) as in Burgundy and Saarland. FAIRHURST's observations in Britain require confirmation: the case in Britain needs more

Source : MNHN, Paris

investigations, particularly using cultures. Freshly moulted spring sch♂ might be ss ones (sch♂ in autumn of the year y giving ss in spring y+1?).

In both cases (a and b) one can admit the possibility of a double production of LL sch♂ and SL ones (Fig. 1), the number of the SL sch ♂ being variable. For instance, the SL may be either few or absent (case a) or more frequent (case b) as in the Allgau mountains (if appearances correspond to realities). Besides his Allgau results, VERHOEFF (1923, 1925) obtained SL in 1922 (an adult collected on 24. 4. 1922 which turned into a SL on 12. 6. 1922 and then into an adult on 15.9.1922).

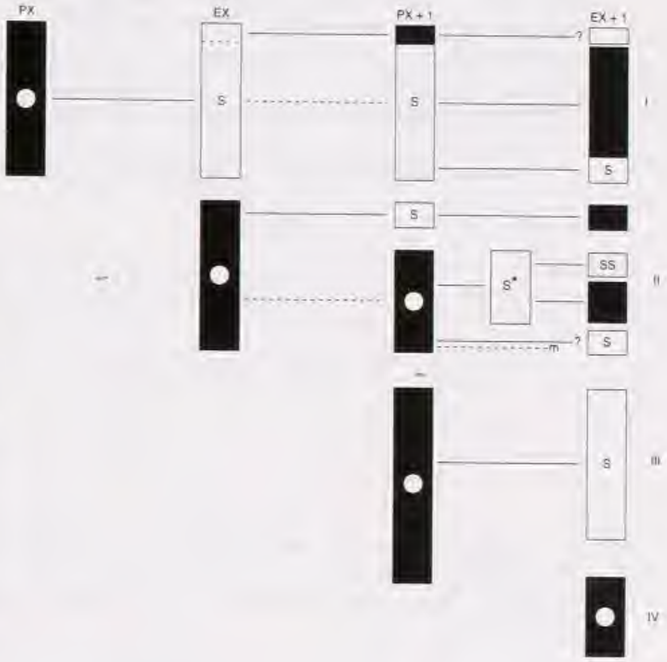


FIG. 1. — Cycle of males in *T. niger* in Germany and Burgundy. The figure takes into account possibilities of both LL and SL intercalaries. **I**: males which became ad1 in spring of year x (Px). **II**: males which became ad1 in summer/autumn x (Ex). In **I** and **II** it is arbitrarily assumed that the number of spring ad1 (ad1 = solid rectangles with an open circle; ad2 = entirely solid rectangles) in year x is equal to the number of summer/autumn ad1 of year x (under this assumption the solid rectangles in PX and EX are of equal dimensions). **III** and **IV**: new generation (of year x+1). In **III** and **IV** it is arbitrarily assumed that the number of spring ad1 (III) is much higher than the number of summer/autumn ad1 (IV) (under this assumption the solid rectangles with an open circle are of different dimensions). Sch♂ are represented by open rectangles. Dashed lines: without moult or transformation; solid lines: transformation after a moult. - m: death, ss: double intercalary form. Asterisk: sch♂ at the end of the spring/beginning of summer (after VERHOEFF, 1923).

Bear in mind that two strategies can be used by Mediterranean *O. sabulosus*: type 1 = MMJ at the end of winter/onset of spring, i.e. a long time before egg-laying in summer/autumn; type 2 = MMJ at the end of spring/summer of the year x, just before mating and egg deposition (SAHLI, 1986, 1991a, b, c, 1992). Nevertheless, in *O. sabulosus* MMJ of type 1 or 2 (or both) and egg-laying take place the same year. The respective strategies used by *T. niger* (at low altitudes in Germany and in Burgundy) and *O. sabulosus* in the South-East of France are not strictly superimposable: this is the reason why we speak of cases a and b in *T. niger* and types 1 and 2 in *O. sabulosus*.

In the Département des Hautes-Alpes (1000 - 1600 m) the production of ad. and sch♂ males (collected under snow bridges or stones) might take place as it does in the case a (SAHLI 1970 & unpubl.), at least in the present state of the investigations. In the Pyrénées ariégeoises, the production of ad-sch♂ might correspond to case b, sch♂ being numerous in autumn according to preliminary observations. A thorough study, over numerous years, needs to be carried out in the Hautes-Alpes, in the Pyrénées ariégeoises and in the Hautes-Pyrénées (in which, on the slopes of the Pic de Campbielh, sch♂ as well as ad males are frequent under stones at the end of the summer).

Although simplified, Tables 5 & 6 allow the interpretation of virtually all the innumerable field and culture data accumulated, be it in spring (year x+2 in Table 5) or in summer/autumn (year x+1, Table 6).

Source : MNHN, Paris

In spring (x+2) the sch♂ number will depend of the number of ad1 of year x+1, which were produced in spring x+1. If one supposes, for instance that these ad1 were numerous, the supposed situation will lead to numerous LL, shown in bold type in Table 5.

TABLE. 5. — *T. niger* in Saarland and Burgundy. Starting from spring ad1. The predominancy - hypothetically assumed - is expressed in bold type. Concerning sch♂, one has assumed (arbitrarily) that the LL (case a) are predominant. Year x+2 will include on the one hand new ad1 (year x+2), assumed (arbitrarily) to be predominant; and on the other hand, mainly slow ad2 (year x) as well as LL (year x+1) (slow ad2 = arising from LL; fast ad2 = arising from SL). The possibilities of ss (from LL in autumn x+1) and the appearance of new ad1 (year x+ 1) have not been taken into account. aut: autumn; n: new; sp: spring.

spx	aut x	sp x+1	aut x+1	sp x+2	
			———	some fast ad2	(x)
	——— sch♂ (SL) ———	some fast ad2 ———	s2 ······	s2 (LL)	(x)
			———	ss	(x)
ad1					
	——— sch♂ (LL) ······	**sch♂ (LL)** ———	**ad2** ······	**slow ad2** ······	(x)
				new ad1	(x+2)
			ad1 n ······	"old" ad1	(x+1)
			———	some fast ad2	(x+1)
			······	**sch♂ (LL)**	(x+1)

TABLE. 6. — *T. niger* in Saarland and Burgundy. Starting from spring of year x+1. The following autumn, slow ad2 (bold) are assumed (arbitrarily) to be well represented. The number of new autumn (x+1) ad1 is variable: compared with the number of s1 (autumn year x+1), it can be higher (in this case ad1 would be in bold letters) or lower (s1 would be in bold).

spring x+1	autumn x+1	
some fast ad2	s2	(x)
sch♂ (LL)	**slow ad2**	(x)
	new autumn ad1	(x+1)
new spring ad1	s1	(x+1)

As a general rule in spring and in case a, the ratio ad1/sch♂ in spring x+2 (Table 5, Fig.1), will depend on:

(a) the number of "new" ad1 (i.e. the number of "new" freshly MMJ) in year x+2, plus the number of possible "old" ad1 from autumn x+1 (MMJ in autumn x+1) which have remained winter ad1 without moulting. These new ad1 can be high, middle or low in number.

(b) the number of LL s1 (which became s1 in autumn x+1). LLs1 in turn depend on the number of ad1 in spring x+1. A few SL s1 (? in Fig.1) might add to the LL s1, as well as some ss (repetitive sch♂).

The number of ad1 - new ones in spring x+2 and/or old ones from autumn x+1 (i.e. ad1 which remain adults without moulting in spring x+2) - often outnumber, more or less, the number of LL s1 or the number of all sch♂ (LL s1 + ? SL s1 + ss).

It is worth noting that in spring x+2 one does not compare males from the same year: in fact *one compares ad1 and LL s1 which became, respectively, adults and intercalaries in two different years.*

Source : MNHN, Paris

Even ad1 (e.g. belonging to stadium 7RO) collected in spring x+2 can be either males which became ad1 in spring x+2, or "old" ad1 which became 7RO adults the previous autumn: succession 7RO autumn ad1 .... 7RO spring ad1 (Table 7).

TABLE. 7. — Development and cycles of males of *T. niger* in Saarland and Burgundy, represented in a highly simplified way. Cases 1, 2, 3: starting from juvenile male (juv), with 6RO in summer/autumn (aut) x+1. - Cases 4, 5, 6: starting from juv or ad1, with 7RO in summer/autumn x+1. - Cases 7 to 12: males of the new generation (G) - i.e. ad1 or juv in spring x+3 - are represented. Only the case of LL sch♂ (and not that of SL ones) has been taken into account. Males from the generation of year x-1 have not been represented. First adults are underlined at the time they become ad1. Dashed line means a moult. Dotted line means no moult.

	autumn x+1		spring x+2		autumn x+2		spring x+3				autumn x+3		
	6RO	7RO	6RO 7RO	8RO	6RO 7RO 8RO	9RO	7RO	8RO	9RO	10RO	8RO	9RO	10RO
1	juv	--------	------ ad1	---------	----- ------ s1	....	....	s1	--------	-------	--------	ad2	
2	juv	---------	----- juv	---------	----- ------ ad1	....	....	ad1	--------	-------	--------	s1	
3	juv	---------	------ juv	---------	------ ------ juv	---------	--------	---------	ad1	-------	--------	---------	s1
4		juv	------ ---------	ad1	----- ----- ---------	s1	....	....	s1	-------	--------	---------	ad2
5		juv----	------ ---------	juv----	----- ----- ---------	ad1	....	....	ad1----	-------	--------	---------	s1
6		ad1	...... ad1	---------	----- ------ s1	....	....	s1	--------	-------	--------	ad2	
7	(new G)						*ad1*	---------	--------	-------	s1		
8							juv	---------	--------	-------	ad1		
9							juv	---------	--------	-------	juv		
10								*ad1*	--------	-------	--------	s1	
11								juv	--------	-------	--------	ad1	
12							ad1	---------	--------	-------	s1		

In other words, in the case of LL, the intercalaries produced in summer/autumn of year "y" will not be "useful" for the reproduction which takes place in spring of the following year y+1. They will be able to reproduce - as ad2 - in spring of year y+2 (or in autumn of year y+1).

The above mentioned ad2 will add to the ad1 possibly produced in year y+2. When the new (= freshly) ad1 are few, we will observe situations like those found in Burgundy (France) near Chamboeuf and in the "Combe de Sainte Foi" (SAHLI, 1989): in these sites the postadult males (mostly ad2) were well represented in spring 1988.

In order to better unterstand the difference between LL and SL, let us add the following comment: if we were in the presence of SL (instead of LL) produced in autumn of year y, the males could mate the following spring y+1, after becoming postadult males (instead of staying intercalaries).

Contrary to SAHLI's 1967 statement, LL s1 may sometimes outnumber ad1, in spring. Such a case has been observed in the forest glade of Segrois ("Sommière de Segrois" near Chamboeuf, Côte-d'Or, France), March 30-31, 1985. In this case, the number of ad1 produced in spring 1985 was low (the winter 1984-1985 was exceptionally cold).

Summer/autumn (Table 6 and Fig. 1) is the main (or even exclusive) "season" of sch♂production (e.g. ad. sch♂) in Saarland (epigean animals) and in Burgundy. At this time of the year, the s1 (which have just become sch♂) may outnumber the newly appeared ad1 under two conditions (Table 6): (a) if the number of newly produced ad1 is low and (b) if the new spring ad1 of year x+1 were well represented. Such a case was observed in Wadrill (15. 9. 1957).

Source : MNHN, Paris

TABLE 8. — Simplified table of the cycles in males (A, C) and females (B) of *T. niger* in Saarland and Burgundy (only some of all the possibilities are given). Among other things, one can see when ad1 males appear (9RO males have not been represented). The possibility of 3RO larvae in autumn of the year x is not indicated. In A brackets mean ad2 originating from SL. In C, generation x-2. ED = Egg Deposition, N.G. = New Generation. Dashed line means a moult. Dotted line means no moult.

ED	Autumn x	Spring x+1	Autumn x+1	Spring x+2	Autumn x+2	Spring x+3
A				7RO	8RO	8RO 9RO 10RO
	4RO	5RO	6RO	ad1 ----------	sch♂ →	sch♂
					↘ ----------	---------- (ad2)
				♂Juv ----------	ad1	ad1
	5RO	6RO	7RO	8RO	9RO	9RO
			♂Juv	---------- ad1	---------- sch♂	.... sch♂
						10RO
					sch♂	---------- -------- (ad2)
			♂ ad1···	ad1		
				N.G.	6RO ♂Juv	
					7RO ♂Juv	
					7RO ♂ad1	
B			6RO	7RO	7RO	
				----------	---------- 8RO	
			7RO	---------- 8RO	.... 8RO	
					---------- 9RO	
				N.G.	6RO	
					7RO	
C		ad1 7RO----------	sch♂ 8RO·······	sch♂ 8RO-------	--------ad2 9RO	.... ad2 9RO
			7RO	7RO	8RO 9RO	9RO
			ad1	ad1 ----------	s1→ ---- ad2	.... ad2
					↘ --- ss·······	.... ss
						(8RO)
					s1 ······	s1

At low altitude in Saarland (epigean animals) - and probably in different regions of Germany, like Eifel, Taunus, Hunsruck, Hesse - and in Burgundy, summer and autumn typically constitute the time at which sch♂ are produced in *T. niger* (case a). Consequently sch♂ may be well represented in autumn (SAHLI, 1967). But, paradoxically, this is not always the case - at least apparently. Thus the number of ad1 can prevail over that of s1 when, for instance, the autumn ad1 production (year x+1, Table 6) was good. Such a case was observed at Wadrill (30.9.1962). In other words, the number of new autumn ad1 can prevail over autumn s1 of year x+1 (Table 6) when the production of spring ad1 of year x+1 was low.

Until recently, we had not understood what really happens in nature in *T. niger* (SAHLI 1966, 1967, 1970). Tables 5-8 and Figure 1 allow us to explain all previous field observations and culture results.

In *T. niger* the predominance of LL Sch♂ over SL (case a) might correspond to a sexual rest period (Table 9) in females (in the sense that females cannot be fertilized each year) - a rest period of one or several years, during which females may elaborate new ripe eggs. In other words, a female "indirect iteroparity" (SAHLI, this volume) might be another *raison d'être* of LL sch♂ and repetitive ones, which are male forms able to withstand harsh conditions (SAHLI, 1991c). Nevertheless, another hypothesis can be put forward: a splitting up and spreading of ♀♀ ad1 (and of egg depositions) over several years might be possible - such a strategy has been called the "CAT strategy" in males (SAHLI, 1990b). The appearance of female ad1 (from a single generation) during several years has been considered in mediterranean*O. sabulosus* (SAHLI, 1991b).

Source : MNHN, Paris

TABLE 9. — *T. niger* in Burgundy and Saarland. Indirect iteroparity (hypotetically admitted) in females, combined with LL in males is represented. The year x+1 during which no egg deposition occurs, is labelled "sexual rest" period and corresponds to the time needed for a new egg production; sum/aut: summer/autumn.

x		x+1		x+2
spring	sum/aut	spring	sum/aut	spring
♂♂ ad1 --------------------	s1	s1 LL --------------------	ad2	ad2
♀♀ first egg deposition	ad1	"sexual rest" period		2nd egg deposition

BLOWER (1969) & coll. (1964, 1974, 1977) had the great merit to introduce the notion of female iteroparity in myriapodology. Nevertheless this is only an hypothesis, and not a well established fact. I have partly adopted BLOWER's idea, at least as a working hypothesis. SAHLI (1993) subdivided it into (a) a direct iteroparity (egg deposition occurs in two consecutive years) and (b) an indirect one (the first egg deposition is separated from the second by an interval of over 2 or 3 years). The possibility of an indirect female iteroparity - with presence of LL sch♂ and R ones - has been suggested (SAHLI, 1993) in the case of the Pyrenean cave blaniulid *Typhloblaniulus lorifer consoranensis*, particularly because of the low temperatures which exist in these caves. The same reasoning can be applied to *T. niger*, which lives rather in relatively "cold" regions. The South limit in France seems to be the Département de la Saône-et-Loire. This species can be found further south in France at higher altitudes (particularly in the south-west, in the Pyrenees). In spite of periodomorphosis, *T. niger* is far less adapted to a hot and dry climate (e.g. of the Mediterranean type) than *O. sabulosus*.

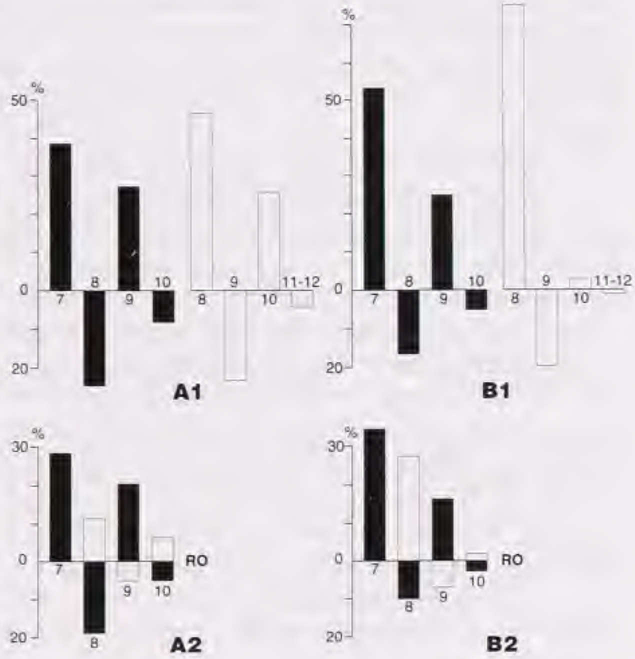


FIG. 2. — *T. niger*. **A**: at Wadrill (Saarland, Germany). **A1**: stadium and specific sexual (ad or sch♂) frequencies of adult males (solid) and intercalaries (open), respectively at each stadium, from stadia 7 to 12RO. [e.g.: in stadium 8RO: ratio 8RO ad1 ♂/all adult ♂ (184); or: 8RO sch♂/all sch♂ (92)]. The frequencies are established from 184 ad ♂ and 92 sch♂, respectively , collected between September 1957 and 1963 (inclusive). **A2**: total frequencies of ad ♂ and sch♂, established from 375 individuals (ad♂ + sch♂) collected between May 1957 and 1963 (inclusive) [e.g. ratio 7RO ad ♂/375 or ratio 8RO sch♂/375. **B**: at Cîteaux (Burgundy,France). **B1**: stadium and specific sexual frequencies of ad ♂ (204) and sch♂ (115) collected in 1963 and 1964. **B2**: total frequency of ad♂ (204) and sch♂ (115), according to 319 individuals collected in 1963 and 1964.

Figure 2 shows the ratios of adults and sch♂ at two Burgundy sites. Notice, particularly at Cîteaux (a) the lower percentage of s2 intercalaries (typically stadium 10RO when ad1 appear at 7RO) compared with the percentage of s1 (stadia 8 and 9RO) and, correlatively, (b) the lower

Source : MNHN, Paris

percentage of postadult ad2 males (a mixture of stadia 9RO males *pro parte* and possibly 10RO males *pro parte*). Drawing a parallel between ad2 and ad1 is in fact a comparison between animals which became adults at two different years; in this respect, one has to take into account the comment made before and Tables 5 & 6. Moreover, stadia 9 and 10RO may comprise not only ad2, but also ad1 (SAHLI, 1989). As for 12RO s3, they are very few: they imply some rare ad4 at both sites.

CONCLUSION

Taking into account the author's experimental results and observations, as well as those of VERHOEFF, in the present state of our knowledge, the following statements can be made. In good conditions and at low altitude in Burgundy and in Saarland, a majority of 7 and 8RO ad1 is able to turn into s1. The s1 are, in the majority, able to give either ad2 or ss. Then a fall seems to appear: only a part of the ad2 are able to turn into s2 and afterwards into ad3 - the relative importance of ad2 depends more or less on the temperature. A very low number of ad3 is able to give s3 and then ad4 (the number of s3 and ad4 seems to increase with altitude and depends on thermic conditions).

If one takes into account only the existence of LL all over the cycle and if the starting point for ad1 takes place in spring of the year y, then males will become ad4 in autumn of year y+4. If ad1 are 2 years old and possess 7RO, the ad4 might in theory be 6 years old, with 13RO; in the "Cirque de Gavarnie", in the Pyrenees at 2500m alt. and over, the oldest adult male with a ring formula of 72/2 (BROLEMANN, 1927) might belong to a stadium equivalent of 23RO (SAHLI, 1969).

Concerning *T. niger*, three comments will be added.

a) A possible dispersal - in time and space - variable for the male categories from one year to the next one, has to be taken into account. Spring sch♂ which became sch♂ the previous autumn y may have dispersed the year y in a given direction, while new ad1 which became adults in spring y+1 may disperse in another direction year y+1. In other words the dispersion areas in years y and y+1 might be different. So animal collections from a single locality may be biased.

b) Intercalaries can sometimes be more or less grouped or "gathered" (cf. SAHLI, 1991a in *O. sabulosus*). In Burgundy and Saarland *T. niger*, in spring and in case a, the activity of LL sch♂ and R individuals may be lower - because they do not moult in spring and do not search for females - than in new spring adult males. New spring adult ♂♂ are very active for two reasons (α) in spring they have just moulted (β) they move in order to search for females for spring mating (for an account of male activity in general, see SAHLI, this volume). FAIRHURST (1968) stated that, in Britain, *Tachypodoiulus* spring sch ♂ - which, according to him, have just moulted in spring (= SAHLI's case b?; thus they might be SL - or ss?) - would, in spite of the moult, have a lower activity than spring adult males. FAIRHURST may be right. But field (or laboratory) experiments should be carried out. With experimental animals in equal numbers, the activity of fresh spring sch♂ (s1 -and not ss) should be compared with that of fresh spring ad♂(ad1) in England and in *Tachypodoiulus*; if, under these conditions, there is a difference, then it can be attributed to sexual activity.

c) Due to the lengh of time of LL or R sch ♂ states - thus to the long length of time between the appearances of ad1♂ and ad2♂ - it is not impossible that a loss of individuals might occur. If a loss really happens, it might be higher in LL and R sch♂ of *T. niger* than in SL of Mediterranean *O. sabulosus*.

Source : MNHN, Paris

REFERENCES

BAKER, G. H. , 1978. — The post-embryonic development and life history of the millipede, *Ommatoiulus moreletii* (Diplopoda: Iulidae), introduced in south-eastern Australia. *J. Zool. Lond.*, **186** : 209-228.

BAKER, G. H., 1984. — Distribution, morphology and life history of the millipede *Ommatoiulus moreletii* (Diplopoda: Iulidae) in Portugal and comparisons with Australian populations. *Aust. J. Zool.*, **32** : 811-822.

BLOWER, J. G., 1969. — Age structures of millipede populations in relation to activity and dispersion. *In : The Soil Ecosystem, Syst. Ass. Publs.*, **8** : 209-216.

BLOWER, J. G. & GABBUTT, P. D., 1964. — Studies on the millipedes of a Devon oak wood. *Proc. Zool. Soc. Lond.*, **143** : 143-176.

BLOWER, J. G. & MILLER, P. F., 1974. — The life cycle and ecology of *Ophyiulus pilosus* (Newport) in Britain. *Symp. Zool. Soc. Lond.*, **32** : 503-525.

BLOWER, J. G. & MILLER, P. F., 1977. — The life-history of the julid millipede *Cylindroiulus nitidus* in a Derbyshire wood. *J. Zool. Lond.*, **183** : 339-351.

BROLEMANN, H. W., 1927. — Myriapodes du cirque de Gavarnie et note sur les vulves de trois d'entre eux. *Bull. Soc. Hist. nat. Toulouse*, **56** : 531-548.

FAIRHURST, C. P., 1968. — Life cycles and activity patterns of schizophylline millipedes. Ph. D. Thesis, University of Manchester, 407 pp.

FAIRHURST, C. P., 1974. — The adaptive significance of variations in the life cycles of schizophylline millipedes. *Symp. zool. Soc. Lond*, **32** : 575-585.

HALKKA, R., 1958. — Life history of *Schizophyllum sabulosum* (L.) (Diplopoda, Iulidae). *Ann. Zool. Soc. Fenn. "Vanamo"*, **19** : 1-72.

HOPKIN, S. P. & READ, H., 1992. — *The biology of millipedes*. Oxford, Oxford Univ. Press, 233 pp.

SAHLI, F., 1966. — Contribution à l'étude de la périodomorphose et du système neurosécréteur des Diplopodes Iulides. Thèse de Doctorat ès-Sciences Naturelles, Université de Dijon, BERNIGAUD & PRIVAT, 226 pp.

SAHLI, F., 1967. — Sur la fréquence des mâles intercalaires du Diplopode *Tachypodoiulus albipes* (C. L. Koch). *C. R. Acad. Sc. Paris, sér. D.*, **264** : 618-620.

SAHLI, F., 1969. — *Contribution à l'étude du développement post-embryonnaire des Diplopodes Iulides*. Ann. Univers. saraviensis, Berlin, Stuttgart, Gebr. Borntraeger, 154 pp.

SAHLI, F., 1970. — Altitude et mâles intercalaires chez le Diplopode *Tachypodoiulus albipes* (C. L. Koch). *C. R. Acad. Sc. Paris, sér. D.*, **271** : 2175-2178.

SAHLI, F., 1986. — Influence des orages sur certains déplacements d'*Ommatoiulus sabulosus* (L.) (Myriapoda, Diplopoda, Julida) dans les Alpes-Maritimes. *Bull. sci. Bourg.*, **39** : 55-57.

SAHLI, F., 1989. — The structure of two populations of *Tachypodoiulus niger* (Leach) (Myriapoda, Diplopoda, Julida) in Burgundy and some remarks on male periodomorphosis. *Rev. Ecol. Biol. Sol*, **26** : 355-361.

SAHLI, F., 1990a. — Recherches sur le cycle des mâles et la fréquence des intercalaires d'*Ommatoiulus sabulosus* (Myriapoda, Diplopoda, Julidae) en Bourgogne. Inversion expérimentale du nombre des intercalaires et des adultes en automne. *Bull. sci. Bourgogne*, **45** : 51-59.

SAHLI, F., 1990b. — On post-adult moults in Julida (Myriapoda, Diplopoda). Why do periodomorphosis and intercalaries occur in males? *In* : A. MINELLI, *Proc. 7th Intern. Congr. Myriapodology*, Leiden, Brill : 135-156.

SAHLI, F., 1991a. — Recherches sur le cycle des mâles d'*Ommatoiulus sabulosus* (L.) (Myriapoda, Diplopoda, Julidae) dans les Alpes-Maritimes et en Provence. Remarques sur les rapports entre la périodomorphose et l'altitude. *Bull. sci. Bourg.*, **44** : 33-39.

SAHLI, F., 1991b. — Fréquence de la périodomorphose chez le Diplopode Julide *Ommatoiulus sabulosus* (L.) dans les Alpes-Maritimes et en Provence : II Passages mâles intercalaires - mâles adultes. *Bull. sci. Bourgogne*, **44** : 41-47.

SAHLI, F., 1991c. — Augmentation et production expérimentales de mâles intercalaires chez des Diplopodes Julida. Note préliminaire. *C. R. Acad. Sci. Paris, Sér. III*, **313** : 59-63.

SAHLI, F., 1992. — On male reproduction strategies in *Ommatoiulus sabulosus* (L.) in the Maritime Alps and Provence (France) : juvenile to adult maturation moults. *Ber. nat.-med. Verein, Innsbruck*, **suppl. 10** : 167-176.

SAHLI, F., 1993. — Signification de la périodomorphose et des intercalaires mâles et femelles chez les Diplopodes Blaniulides cavernicoles pyrénéens. *Mém. Biospéol.*, **20** : 209-215.

VERHOEFF, K. W., 1915. — Zur Kenntniss einiger alpiner Chilognathen. *Zool. Anz.*, **45** : 219-238.

VERHOEFF, K. W., 1916. — Abhängigkeit der Diplopoden und besonders der Juliden-Schaltmännchen von äusseren Einflüssen. *Z. wiss. Zool.*, **116** : 535-586.

VERHOEFF, K. W., 1923. — Periodomorphose. *Zool. Anz.*, **56** : 233-238 & 241-254.

VERHOEFF, K. W., 1925. — Mediterrane Chilopoden und Notiz zur Periodomorphose der Juliden. *Zool. Anz.*, **64** : 63-80.

Source : MNHN, Paris

VERHOEFF, K. W., 1928. — Diplopoda 1. *In* : H. G. BRONN's *Klassen und Ordnungen des Tierreichs*, **5**, Leipzig, Akademische Verlagsgesellschaft : 1-1072.

VERHOEFF, K. W, 1932. — Diplopoda 2. *In* : H. G. BRONN's *Klassen und Ordnungen des Tierreichs*, **5**, Leipzig, Akademische Verlagsgesellschaft : 1073-2084.

VERHOEFF, K. W., 1934. — Ueber Diplopoden der allgauer Alpen, deutsche Craspedosomidae und Periodomorphose. *Zool. Anz.*, **108** : 27-40.

Source : MNHN, Paris

cAMP Influence on Brain and Germinal Cells RNA Syntheses in *Lithobius forficatus* (L.): an Autoradiographic Study

Michel DESCAMPS *, *Catherine* JAMAULT-NAVARRO ** & *Marie-Chantal* FABRE *

* Ecophysiologie d'Invertébrés du Sol, Laboratoire de Biologie Animale, Université de Lille I, F-59655 Villeneuve d'Ascq Cedex, France (to whom all correspondence must be sent)
** Laboratoire de Biologie Animale, UFR Sciences Exactes et Naturelles, Université de Picardie, 33 rue Saint-Leu, F-80039 Amiens Cedex, France

ABSTRACT

Mature *L. forficatus* were injected with 2 nmol of dibutyryl cAMP (sodium salt) [dBcAMP]. Animals of day 1, 2, 3 and 7 after injection were investigated. Autoradiographs were analysed either by cytophotometry (Leitz MPV) or by image analysis (Biocom 2000 device). *Germinal cells*: in oocytes, the supply of dBcAMP led to a significative increase in [^{3}H]-uridine uptake during the first 3 days of the experimental series. Nevertheless, on day 7, control values were obtained. In spermatocytes, two cases must be reported: if the testes were not in a phase of active spermatogonial divisions ("phase de reconstitution"), an increase in RNA syntheses was observed. At the opposite of that measured for oocytes, the maximum of label was observed on day 7. For testes with active mitoses, the uptake remained at a low level, either in controls or in dBcAMP injected animals. *Brain*: analysis performed on various areas (middle and lateral parts of the so-called *pars intercerebralis*, frontal lobes and cerebral glands) showed that dBcAMP has a stimulating effect on the uptake of the tritiated precursor. The increase of RNA syntheses observed in germinal cells and in neurons shows that cAMP is a good candidate to be the second messenger of the stimulating neuropeptide(s) issued from *pars intercerebralis* neurosecretory cells. Our results have, in addition, shown that a refractory period occurs during the period of active mitoses in the testis.

RÉSUMÉ

Influence de cAMP sur la synthèse de l'ARN du cerveau et des cellules germinales chez *Lithobius forficatus* (L.): étude autoradiographique.

Après injection de 2 nmol de dibutyryl cAMP (sel de sodium) [dBcAMP], des adultes matures de *Lithobius forficatus* ont été étudiés aux jours 1, 2, 3 et 7. Les autoradiographies analysées, soit par cytophotométrie, soit par un analyseur d'images Biocom 2000, montrent que les ovocytes incorporent significativement plus d'uridine tritiée que les témoins durant les 3 jours qui suivent l'injection de dBcAMP. Des valeurs témoins sont cependant récupérées au jour 7. En ce qui concerne les spermatocytes, deux cas se présentent : si le testicule n'est pas en phase de reconstitution (période de divisions goniales), une augmention des synthèses d'ARN est observée. Aucune augmentation de synthèse n'est observée si de nombreuses divisions goniales sont en cours dans le testicule. Les analyses effectuées sur différentes zones du cerveau (*pars intercerebralis*, lobes frontaux) ou sur la glande cérébrale, montrent un effet stimulateur sur l'incorporation

DESCAMPS, M., JAMAULT - NAVARRO, C. & FABRE , M.-C., 1996. — cAMP influence on brain and germinal cells RNA syntheses in *Lithobius forficatus* (L.): an autoradiographic study. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 385-390. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

du précurseur tritié. L'augmentation des synthèses d'ARN observée aussi bien dans les cellules germinales que dans le système nerveux montre que l'AMP cyclique est sans doute le second messager du (des) neuropeptide(s) issu(s) des cellules neurosécrétrices de la *pars intercerebralis*. Nos résultats montrent en outre l'existence d'une période réfractaire à l'action de l'AMP cyclique.

INTRODUCTION

In *Lithobius*, the endocrine control of gametogenesis is the result of the balance between stimulating factors - ecdysteroids and a hormone issued from *pars intercerebralis* neurosecretory cells (pi NSC) - and a moderating one released from the cerebral glands (neurohemal cephalic organs) (reviews: JOLY & DESCAMPS, 1988; DESCAMPS, 1992a). In addition, in females, it has been shown that too high levels of ecdysteroids triggers the release of the moderating factor (DESCAMPS, 1992b). It has been previously demonstrated that cAMP was present in testes and that the level of this messenger was increased, except during meiosis, after electrical stimulation of the pi NSC (DESCAMPS *et al*, 1986). So, it was of interest to proof the effects of cAMP on germinal cells and on brain neurons metabolism, in order to compare the results to those obtained after electrical stimulation or ecdysteroid injection.

MATERIAL AND METHODS

The experiments were conducted on mature *Lithobius forficatus* (L.) collected in northern France, during autumn, in order to have animals showing a low rate of RNA syntheses, at least in male germinal cells.
Animals were injected with 2 nmol of dibutyryl cAMP (sodium salt) [= dBcAMP; purchased from Sigma] in solution in a saline adapted to chilopods. The autoradiographic study was conducted after the injection of 185 KBq (= 5 µCi) of [^{3}H]-uridine (CEA, France; specific activity 166,5 TBq [= 45 Ci]/mMol) 48 hrs before fixation. The animals were fixed 1, 2, 3, and 7 days after the injection of the dBcAMP. Tissue sections, treated according to FICQ (1961), were covered with Kodak NTB3 emulsion. Kodak D19 was used as developer. The cytophotometric study of the labelling of germinal cells was conducted either with a Leitz MPV cytophotometer, using a 500 µm^2 diaphragm. Only growing spermatocytes (40 to 70 µm in diameter) or vitellogenetic oocytes (stage 2B and beginning of stage 3 according to HERBAUT, 1972) were investigated. Brain endocrine areas were studied with an image analysis device (Biocom 2000). In the graphs concerning the lattest results no error bars are shown, measurements being the results of area labelling expressed as a mean percentage of label of the area (neuropil label is defined as an internal control and fixed to 1) and not as the result of cell types measured individually.

RESULTS

Germinals cells

In oocytes, a significant increase of uptake of [^{3}H]-uridine was recorded in animals of day 1, 2, 3. In day 7 animals the label was comparable to that of the controls (Fig. 1).

In males, two cases were recorded. In animals with a testis showing growing spermatocytes, an increase of uptake was present in all the experimental series (Fig. 2). In the animals that undergo the renewal of their stock of spermatocytes ("période de reconstitution", JOLY & DESCAMPS, 1969), at the opposite of that observed precedently, the level of label was low in controls (*circa* 30 units), and in addition, no effect of dBcAMP was found (label staying between 20 and 25 units).

Brain

In all females, an increase uptake of the tritiated precursor was found in the endocrine areas [median (Fig. 3) and lateral (Fig. 4) parts of the pi, frontal lobes (Fig. 5)]. Nevertheless, the maxima recorded here were different according to the type of NSC studied.

The results were quite different for the cerebral glands. An increased uptake took place during the first three days, a control value was measured from day 7 animals (Fig. 6).

Source : MNHN, Paris

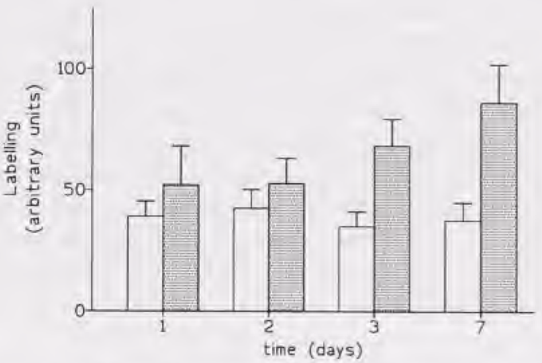


FIG. 1. — Cytophotometric measurements of labelling over oocyte nuclei after 1, 2, 3, 7 days. Means ± SD. Controls: open bars.

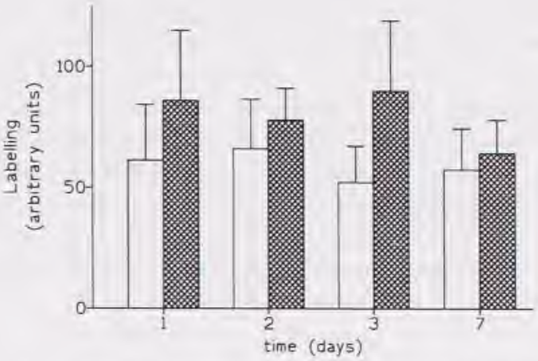
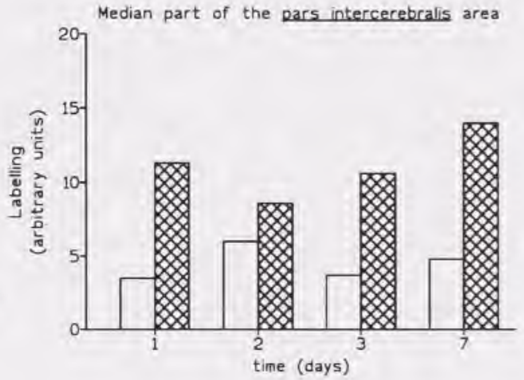
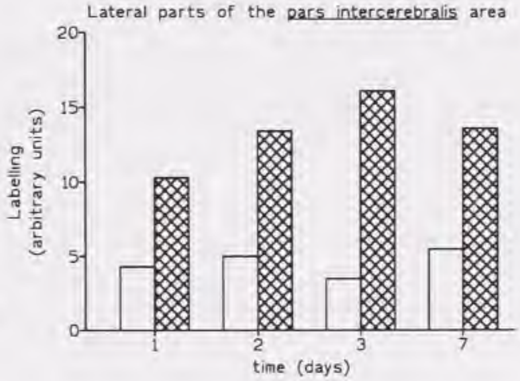


Fig. 2. — Cytophotometric measurements of labelling over spermatocyte nuclei after 1, 2, 3, 7 days. Means ± SD. Controls: open bars.

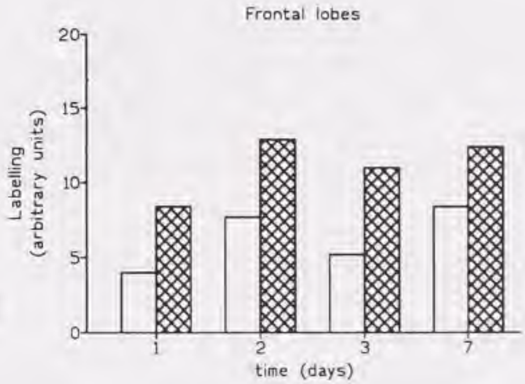
3



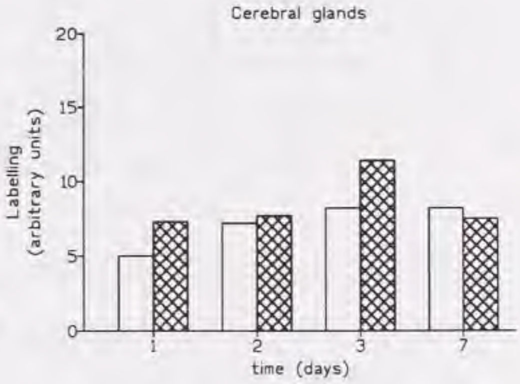
4



5



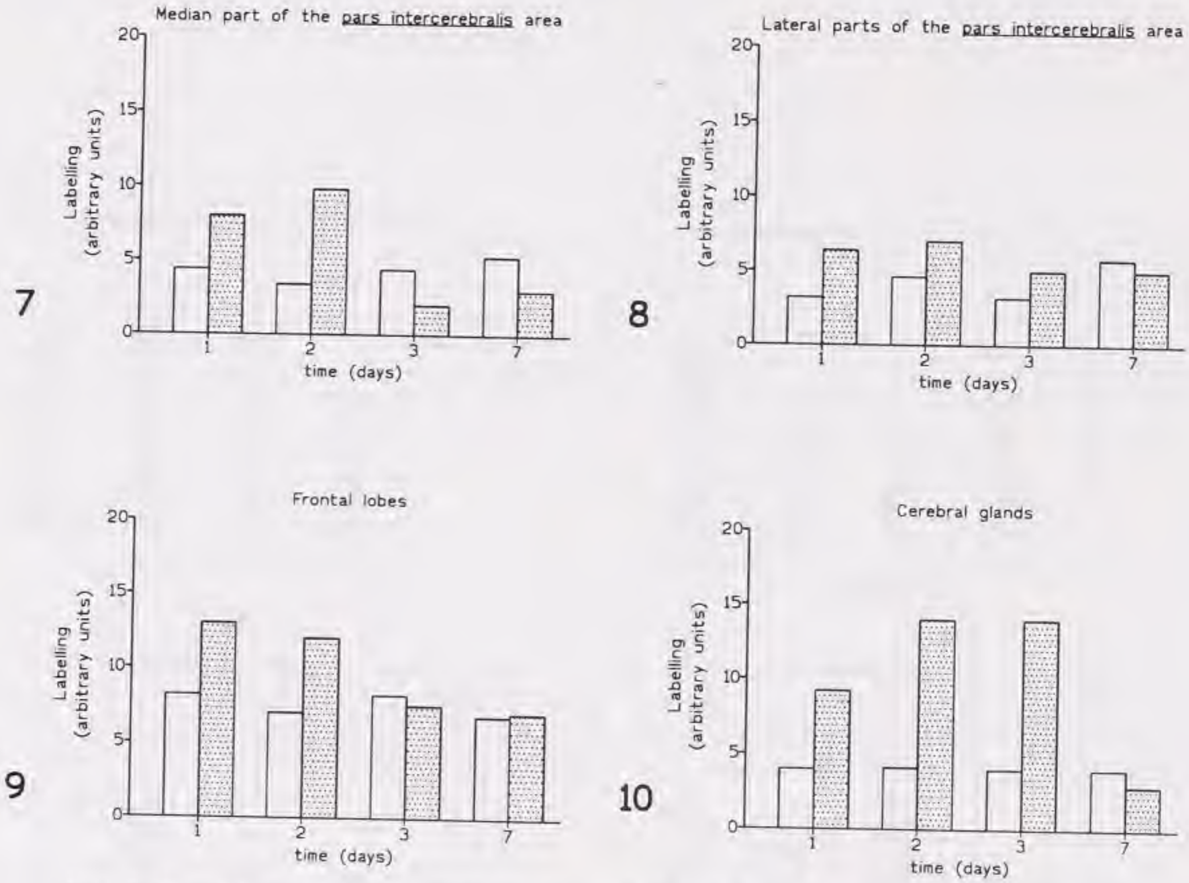
6



FIGS. 3-6. — Mean label of brain endocrine areas of pi and of cerebral glands in females. Controls: open bars.

Source : MNHN, Paris

In males, we can only report the results concerning animals not implied with the renewal of the spermatocyte stock. As a consequence, the label was low over the brain and cerebral gland, but not strong enough to enable measurements by the image analyser. In animal not concerned with this refractory period, an increase in the uptake of [^{3}H]-uridine was observed, but for shorter times than in females. For the median part of the pi, this increase lasted two days. Then, the values recorded were significantly under the control values (Fig. 7). Lateral parts of the pi showed, compared to the controls, increases of uptake, but only during the first three days; nevertheless, it must be noticed that these increases were of less great extend than those recorded for the median part (Fig. 8). In frontal lobes labelling was increased only in the first two days and then control values were recorded (Fig. 9). The most dramatic increases were recorded for the cerebral glands, particularly for animals of day 2 and day 3. In day 7 animals, values recorded were slightly under the control values (Fig. 10).



FIGS. 7-10. — Mean label of brain endocrine areas and of cerebral glands in males. Controls: open bars.

CONCLUSIONS AND DISCUSSION

As a general conclusion, we can say that cAMP stimulates the uptake of [^{3}H]-uridine and can be considered as a good candidate to be the 2nd messenger of various kind of cells as those of NSC or germinal cells.

Source : MNHN, Paris

Stimulation of uptake in oocytes is only transient: this result can be compared to findings after injection of (at least) 0.4 µg of 20-hydroxyecdysone and was explained by the release of a moderating factor, in order to limitate the level of the metabolism and to enable a normal and regular vitellogenesis (DESCAMPS, 1992b). So, also in this case, the release of a moderating factor is more likely involved in the regulatory process, explaining as a consequence the rather short time of increased metabolism in oocytes.

At the opposite, stimulation of spermatocyte metabolism was observed during the whole time of experiment, comparable to previous results (DESCAMPS, 1981, 1991). It appears that, either there is no release of a moderating factor in males, the balance between the stimulating and the moderating hormones being not regulated in the same manner in males and in females, or, as another explanation, the spermatocytes are less sensitive to variations of hormonal levels. They might be protected by the testis blood barrier, the lattest being regulated partly by 20-hydroxyecdysone (BENIOURI, 1984).

Concerning the brain, the increase of tritiated uridine uptake in pi NSC requires more time in females (at least 7 days) than in males (2 or 3 days). This fact can be related to the reproductive physiology of animals: females are in their vitellogenetic phase whereas males are entering in a period of minimal rate of metabolism (the so called winter rest period). Differences between female and male brains were previously evidenced in transplantation experiments on the influence of the *pars intercerebralis* on the gametogenetic cycle (DESCAMPS, 1974), and, at this time, it was suggested that these differences took their origin in the course of gametogenetic cycles. The present results are in full agreement with these statements.

In the frontal lobes, increased values were recorded during the whole time of experimental series for both sexes, whereas in cerebral glands an increase was measured for only the first three days. It is difficult to explain or to relate these findings to physiological events: release of moderating factor by the cerebral gland do not imply increased syntheses, numerous secretory granules being stored in the cells and in the axonal endings of the glands. In short, for the brain, differences are only recorded according to the sex, and this was previously reported in transplantation experiments (DESCAMPS, 1974).

cAMP is involved in various kind of processes. For example, in Crustacea it has been found that the processes of protein synthesis are involved in previtellogenic oocytes (EASTMAN-REKS & FINGERMAN, 1984) and those which are necessary for ecdysteroid production are inhibited by MIH (molt inhibiting hormone) through cAMP (among other authors: MATTSON & SPAZIANI, 1985; SEDLMEIER & FENRICH, 1993). At the opposite, in Insecta, the process of ecdysteroid synthesis is stimulated by PTTH (prothoracotropic hormone) through cAMP (among others: SMITH *et al.*, 1984, 1993).

We have found that, in the brain, stimulating or moderating factors of NSC secreting show both an increased uptake of [^{3}H]-uridine after dBcAMP supply. It is the question if the increase of this uptake that is triggered in NSC frontal lobes is directly induced by the cyclic nucleotide or if the activation of NSC frontal lobes is a consequence of the activation of pi NSC in order to counteract their action in a regulatory process of metabolism? The answer to such a question cannot be given before the localization of adenylate cyclase will be investigated.

REFERENCES

BENIOURI, R., 1984. — Testis blood barrier control by 20-hydroxyecdysone in *Lithobius forficatus* (L.) (Myriapoda, Chilopoda). *Cytobios*, **40** : 159-170.

DESCAMPS, M., 1974. — Etude du contrôle endocrinien du cycle spermatogénétique chez *Lithobius forficatus* (L.) (Myriapode, Chilopode). Rôle de la *pars intercerebralis*. *Gen. Comp. Endocrinol.*, **25** : 346-357.

DESCAMPS, M., 1991. — Role of morphogenetic hormones in spermatogenesis in Myriapoda. *In* : A. P. GUPTA, *Morphogenetic Hormones of Arthropods. Vol. I, part 3: Roles in histogenesis, organogenesis and morphogenesis*. New Brunswick & London, Rutgers University Press : 567-592.

Source : MNHN, Paris

DESCAMPS, M., 1992a — Endocrine events during the life cycle of *Lithobius forficatus* (L.) (Myriapoda, Chilopoda). *Ber. nat.-med. Verein Innsbruck*, **suppl. 10** : 111-116.

DESCAMPS, M., 1992b — Influence de la 20-hydroxyecdysone sur les synthèses d'ARN dans les ovocytes de *Lithobius forficatus* L. (Myriapode, Chilopode). *Bull. Soc. Zool. Fr.*, **117** : 139-147.

DESCAMPS, M., CARDON, C. & LEU, B., 1986. — Influence of brain electrical stimulation or 20-hydroxyecdysone injection on the cAMP level in the testes of *Lithobius forficatus* (L.) (Myriapoda, Chilopoda). *In* : M. PORCHET, J. C ANDRIÈS & A. DHAINAUT, *Advances in Invertebrate Reproduction 4*. Amsterdam, Elsevier Science Publishers : 505.

EASTMAN-REKS, S., FINGERMAN, M., 1984. — Effects of neuroendocrine tissue and cyclic AMP on ovarian growth in vivo and *in vitro* in the fiddler crab, *Uca pugilator*. *Comp. Biochem. Physiol.*, **79A** : 679-684.

FICQ, A., 1961. — *Contribution à l'étude du métabolisme cellulaire au moyen de la technique autoradiographique*. Bruxelles, Inst. Inter. Univ. Sci. Nucl. Belge, Monographie n° 9 : 1-121.

HERBAUT, C., 1972. — Etude cytochimique et ultrastructurale de l'ovogenèse chez *Lithobius forficatus* (L.) (Myriapode, Chilopode). Evolution des constituants cellulaires. *Wilhelm Roux'Archiv*, **170** : 115-134.

JOLY, R. & DESCAMPS, M., 1969 — Evolution du testicule, des vésicules séminales et cycle spermatogénétique chez *Lithobius forficatus* L. (Myriapode Chilopode). *Arch. Zool. exp. gén.* **110** : 341-348.

JOLY, R. & DESCAMPS, M., 1988 — Endocrinology of Myriapods. *In* : H. LAUFER et R.G.H. DOWNER, *Endocrinology of selected Invertebrate Types*, New-York, Alan R. Liss, 429-449.

MATTSON, M. P. & SPAZIANI, E., 1985. — Cyclic AMP mediates the negative regulation of Y-organ ecdysteroid production. *Mol. Cell. Endocrinol.*, **42** : 185-189.

SEDLMEIER, D. & FENRICH, R. 1993. — Regulation of ecdysteroid biosynthesis in crayfish Y-organ : I. Role of cyclic nucleotides. *J. exp. Zool.*, **265** : 448-453.

SMITH, W. A., GILBERT, L. I. & BOLLENBACHER, W. E., 1984. —The role of cyclic AMP in the regulation of ecdysone synthesis. *Mol. Cell. Endocrinol.*, **37** : 285-294.

SMITH, W. A., VARGHESE, A. H. & LOU, K. J., 1993. — Developmental changes in cyclic AMP-dependant protein kinase associated with increased secretory activity of *Manduca sexta* prothoracic glands. *Mol. Cell. Endocrinol.*, **90** : 187-195.

Source : MNHN, Paris

Cadmium Kinetics in *Lithobius forficatus* (L.) during Experimental Contamination and Decontamination

Sylvie GÉRARD, *Marie-Chantal* FABRE & *Michel* DESCAMPS *

Ecophysiologie d'Invertébrés du Sol, Laboratoire de Biologie Animale, Université de Lille I
F-59655 Villeneuve d'Ascq Cedex, France
* to whom all correspondence must be sent

ABSTRACT

Experiments were conducted on adult mature *L. forficatus* specimens collected in an area of Northern France contaminated by various metals (Al, Cd, Cu, Pb). The mean level of cadmium in the soil reached about 60 ppm. Kinetics of decontamination, performed in autumn experiments showed a decrease in Cd level in centipedes, from about 30 ppm at the beginning of the experiment to about 12 ppm ten weeks later. Kinetics of contamination, starting after a period of decontamination, showed at first a dramatic increase in Cd levels (up to a mean 80 ppm), followed by a decrease, although the animals were regularly fed with cadmium contamined larvae. Difference between animals fed or not with cadmium containing diet ranged from 18 ppm to only 8 ppm at the end of the experimental series. Experiments conducted either in autumn or spring showed comparable evolution of level curves, if not the same values.

RÉSUMÉ

La cinétique du cadmium chez *Lithobius forficatus* (L.) au cours d'une expérience de contamination et de décontamination.

Des expériences ont été menées chez des adultes de *Lithobius forficatus* prélevés dans le Nord de la France, dans une zone contaminée par divers métaux (Al, Cd, Cu, Pb). La cinétique de décontamination, suivie expérimentalement durant l'automne, montre une diminution des taux de 30 ppm au début à environ 12 ppm dix semaines plus tard. Les cinétiques de contamination, débutant après une période initiale de décontamination montrent dans un premier temps une augmentation importante des taux atteignant 80 ppm. Une décroissance régulière des taux est ensuite observée, alors que les animaux continuent à recevoir une nourriture contaminée par le cadmium. A la fin de l'expérience, la différence entre les animaux nourris ou non avec de la nourriture cadmiée est d'environ 10 ppm. Aux valeurs près, l'expérimentation, qu'elle soit automnale ou printannière, montre les mêmes phénomènes.

INTRODUCTION

Pollution by heavy metals is one of the main ecological problems of industrial areas, at least for invertebrates (HOPKIN, 1989). In Northern France, numerous metal works were closed during the last 20 years, and after demolition of furnaces and buildings, the resulting industrial wastelands were rehabilited. Part of such a wasteland, located in Mortagne du Nord, previously a zinc works, was used as an experimental area.

GÉRARD, S., FABRE, M.-C. & DESCAMPS, M., 1996. — Cadmium kinetics in *Lithobius forficatus* (L.) during experimental contamination and decontamination. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 391-394. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

It has been shown in a previous work (HOPKIN *et al.*, 1985) that chilopods are one of the invertebrate groups that is common in metal contaminated areas. Despite studies concerning the rate of assimilation of heavy metals by *Lithobius variegatus* (HOPKIN *et al.*, 1985; HOPKIN & MARTIN, 1984), and some other soil arthropods (JANSSEN *et al.* 1991), no data exist about the dynamics of accumulation and detoxication of metals in centipedes.

The present study is part of a program initiated by "Espace Naturel Régional du Nord Pas de Calais" about the biology and evolution of industrial wastelands.

MATERIAL AND METHODS

Animals

Mature adults *Lithobius forficatus* (L.) were collected on the metalliferous grassland located in Mortagne du Nord. For some experimental series, animals of the same subareas were collected separately, the level of cadmium varying according to the place of sampling (reported as "A" [lawn], "B" [stub] and "C" [mixed poplar-willow-birch woodland] in the corresponding graph).

In the lab, the centipedes were fed with *Chironomus* larvae bought at a fisher supplier and maintained either in tap water or in water containing 20 mg/l of $CdCl_2$. When used for feeding, the Cd mean level of the latter was 150 mg/kg. Animals were starved for 3 days before analysis in order to ensure digestion and to not measure the gut content.

Each point of the decontamination or of the experimental contamination curve resulted from four to five animals analysed individually.

Mineralization

Animals were dried at 80°C (12 hrs) and weighed. The samples, reduced to powder, poured into test tubes and added with 1 ml HNO_3 (Normapur) were kept at room temperature. Samples were then warmed up to 120°C and kept at this temperature till half the acid mixture was evaporated. 1 ml of a mixture of HNO_3 - H_2SO_4 - $HClO_2$ (10v/2v/3v; Normapur grade) was then added and warmed up to 180°C. When half the solution was evaporated, the resulting mixture was diluted to 20 ml with deionized water.

The digests were analysed for cadmium by flame (Perkin Elmer 2380) or flameless (Varian AA 300) atomic absorption spectrophotometry. Results are expressed hereafter in mg of cadmium per kg of dry mass.

RESULTS

The mean level in soil was about 40 mg/kg of Cd (ranging from 6 to 76 mg/kg), i.e more than one hundred fold higher than in agricultural soils of Northern France (0.32 mg/kg, data from "Chambre d'Agriculture du Nord", October 1990). As a consequence, animals contained more cadmium than those collected in unpolluted sites (for example, 4.2 mg/kg in another site located in St-Amand, some kilometers southwest of Mortagne *versus* 10 to 30 mg/kg).

Animals fed with unpolluted diet showed a decrease of the level of Cd, as shown by the slope of the linear regression (Fig. 1), evidence for the existence of a detoxication process. Animals fed with Cd polluted diet (after a period of unpolluted feeding) showed a dramatic increase of the Cd level during two weeks, and then decreased values were recorded, with a rate of elimation far higher than that observed in controls (Fig. 2).

At the end of the experimental series, the values recorded in the two kinds of animals were not so different (Fig. 2), controls ranging from 8 to 14 mg/kg and Cd fed animals about 20 mg/kg.

In experiments conducted during spring, only experimental contamination was performed, after about two weeks of natural detoxication in the lab. The same shape of curve was observed, as in autumn experiments: a dramatic increase followed by active decontamination (Fig 3). In this particular case, the area of collection of animals was recorded, so we were able to demonstrate the variations observed from one animal to another, according to the sample site (Fig. 4).

Concerning the assimilation rate of Cd, we have indirect evidence for a quick elimination or, at best, a non assimilation at the time of feeding. Indeed, based on the mean Cd level of the diet, an animal ingested about 5.5 µg Cd per week and the maximum level recorded a week after the beginning of polluted feeding reached a mean 80 mg/kg of dry weigh, corresponding to about 1.6 µg of Cd per centipede, i.e. 1 µg more than at the beginning of the experiment.

Source : MNHN, Paris

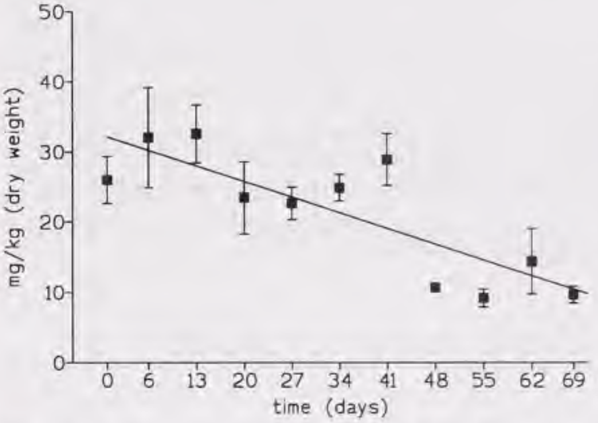


FIG. 1. — Elimination of cadmium in *L. forficatus* fed with unpolluted diet. Original data are given as means with SEM. Solid line: linear regression.

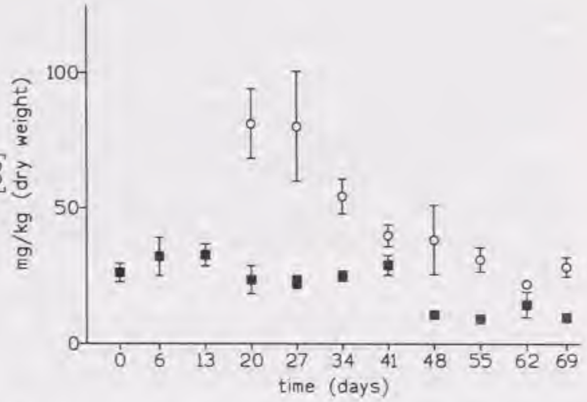


FIG. 2. — Accumulation and elimination of cadmium in *Lithobius*. Black squares: animals fed with unpolluted diet (same animals as in Fig. 1); open circles: animals fed with Cd polluted diet (starting on day 15). Means ± SEM.

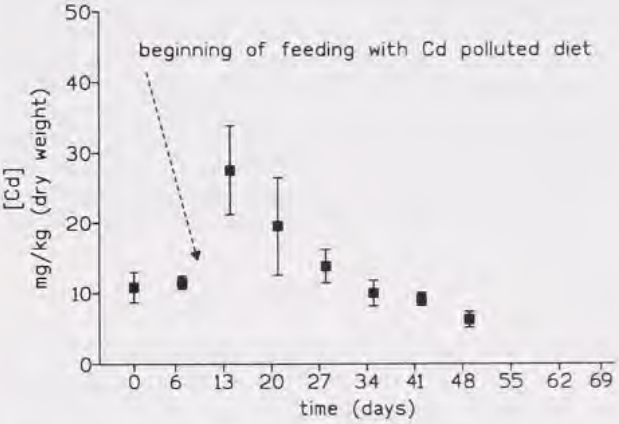


FIG. 3. — Accumulation and elimination of cadmium in *Lithobius* during spring experiments. Feeding with Cd polluted diet starting on day 9. Means ± SEM.

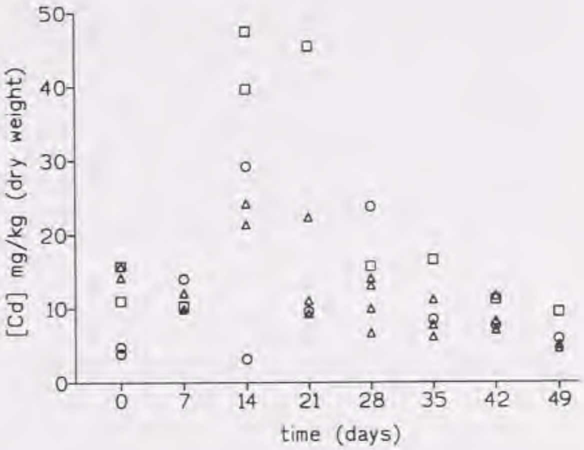


FIG. 4. — Same animals as in Fig. 3, but with individual values according to the sample site (A, B, C; for details, see the text).

DISCUSSION

The first point to discuss is the ability of *Lithobius* to eliminate cadmium. Indeed, we have shown a decrease of the Cd level when animals were supplied with clean diet. This rate of elimination in our autumnal experimental series is about 20 ppm for ten weeks. It must be notice that in spring experiments the level of Cd in animals was a bit lower. This fact may be related to low amounts of metal ingested, consequence of the winter low rate of metabolism and poor feeding.

Source : MNHN, Paris

The second point concerns the dynamics of accumulation: the animals reacted rather quickly to Cd supply. Only two points of analysis show high values: during two weeks the animals accumulate more Cd than they can eliminate. Then, they eliminate more Cd than they assimilate. As the values recorded at the end of experimental series were quite comparable to that measured at the time of collection, we can consider that the latter are equilibrium values for animals when they are in a period of active physiology in metal polluted soil.

The assimilation rate of Cd shown by our results is a little bit higher (about 18%) than the 10% found by HOPKIN *et al.* (1985) but we may keep in mind that the diet was not the same, and that *Chironomus* larvae bring Cd both as compounds linked to the body and as soluble $CdCl_2$ to be found in the water layer surrounding the body.

ACKNOWLEDGMENTS

The present study was supported by a grant from "Espace Naturel Régional du Nord-Pas-de-Calais" and "Fondation de France" concerning the study of "Pelouse métallicole de Mortagne".

REFERENCES

HOPKIN, S. P., 1989. — *Ecophysiology of metals in terrestrial invertebrates.* London, Elsevier Applied Science.

HOPKIN, S. P. & MARTIN, M. H., 1984. — Assimilation of zinc, cadmium, lead and copper by the centipede *Lithobius variegatus* (Chilopoda). *J. Appl. Ecol.*, **21** : 535-546.

HOPKIN, S. P., WATSON, K., MARTIN, M. H. & MOULD, M. L., 1985. — The assimilation of heavy metals by *Lithobius variegatus* and *Glomeris marginata* (Chilopoda; Diplopoda). *Bijdr. Dierk.*, **55** : 88-94.

JANSSEN, M. P. M., BRUINS, A., DE VRIES, T. H. & VAN STRAALEN, N. M., 1991. — Comparison of cadmium kinetics in four soil arthropod species. *Arch. Environ. Contam. Toxicol.*, **20** : 305-312.

Source : MNHN, Paris

Cytochemistry of the Tergite Epicuticle of *Glomeris marginata* (Villers) (Myriapoda, Diplopoda): Preliminary Experimental Results

Philippe COMPÈRE, *Stéphane* DEFISE & *Gerhard* GOFFINET

Université de Liège, Laboratoire de Biologie générale et de Morphologie ultrastructurale
Institut de Zoologie, 22 quai Ed. Van Beneden, B-4020 Liège, Belgique.

ABSTRACT

The present study determines the ultrastructural location of chitin, proteins, and lipids in the epicuticle of the diplopod *Glomeris marginata* (Villers). The results lead to the conclusion that the cuticle includes two functionally different parts: the upper part is involved in the permeability of the cuticle whilst the lower has mainly a mechanical role. The upper part includes three epicuticular layers probably homologous to those described in insects: the cuticulin layer, the wax layer, and the proteinaceous cement layer. The former seems to consist of a median leaflet of stabilized lipid polymers sandwiched in two protein leaflets. This arrangement is assumed to be a primitive, general feature of the arthropod cuticle, having been identified as the main waterproofing barrier in the cuticle of marine decapod crustaceans. The inner epicuticle and the mineralised procuticle play a mechanical role. The inner epicuticle consists of a lipoprotein matrix that surround rod-shaped protein elements and chitin-protein fibres which are probably of procuticular origin. Structurally and functionally, it might be regarded as a structure convergent with that of decapod crustaceans, that plays a part as a reinforcement to prevent the epicuticle splitting off from the mineralised exocuticle.

RÉSUMÉ

Etude cytochimique de l'épicuticule des tergites de *Glomeris marginata* (Villers) (Myriapoda, Diplopoda).

Le présent travail concerne la localisation ultrastructurale de la chitine, des protéines et des lipides de l'épicuticule du diplopode *Glomeris marginata* (Villers). D'un point de vue fonctionnel, les résultats amènent à conclure que la cuticule comprend deux parties différentes : la partie supérieure intervient dans la perméabilité de la cuticule tandis que la partie inférieure joue un rôle essentiellement mécanique. La partie supérieure comporte trois couches épicuticulaires de surface, probablement homologues de celles décrites chez les insectes : la couche de cément protéinique, la couche de cire, et la cuticuline. Cette dernière semble former un feuillet médian de polymères lipidiques stables pris en sandwich entre deux feuillets protéiques. On admet que la cuticuline est un constituant primitif commun à toutes les cuticules d'arthropodes. Elle est reconnue comme la principale barrière imperméable de la cuticule des crustacés décapodes marins. Les couches jouant un rôle mécanique sont l'épicuticule interne et la procuticule minéralisée. L'épicuticule interne consiste en une matrice lipoprotéique entourant des éléments protéiques en forme de batonnets et des fibres chitinoprotéiques d'origine probablement procuticulaire. D'un point de vue structural et fonctionnel, cette constitution de l'épicuticule interne peut être considérée comme une convergence avec celle rencontrée chez les crustacés décapodes, en raison de son rôle de renfort empêchant l'épicuticule de se détacher de l'exocuticule minéralisée.

COMPÈRE, P., DEFISE, S. & GOFFINET, G., 1996. — Cytochemistry of the tergite epicuticle of *Glomeris marginata* (Villers) (Myriapoda, Diplopoda): preliminary experimental results. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 395-401. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

INTRODUCTION

The arthropod cuticle is commonly regarded as an outer integumental structure acting as an exchange surface in addition to providing mechanical protection. From an adaptive and evolutionary point of view, the differentiation of several epicuticular layers with peculiar structures and chemical composition has probably contributed to the success of this group in colonising a wide variety of environments.

As a result, the layers of epicuticle show a high degree of specialisation according to the physiology of the integumental regions and to the habitat. For instance, it is well known that cuticular lipids such as the surface waxes represent a barrier against water loss in terrestrial arthropods such as insects and arachnids (HADLEY, 1981). In this respect, diplopods appear as a very original and interesting group to study, since they are phylogenetically close to insects but live in nearly the same wet microhabitats as terrestrial isopods and possess a mineralised cuticle as it is the rule in numerous crustaceans. Little is known about the structure and especially the chemical composition of the epicuticular layers.

Recent ultrastructural observations of ANSENNE *et al.* (1990), have shown that the organisation of the cuticle of *Glomeris marginata* (Villers) fits the classical scheme known from arthropods. In both the cuticle consists of a thin epicuticle overlying a thick, lamellate procuticle which is subdivided into an exocuticle and an endocuticle. The cuticle is traversed by pore canals and ducts of dermal glands. However, the epicuticle exhibits peculiar features whose interpretation is critical (Fig. 1). The outermost epicuticular layers of diplopods with its cuticulin, wax and cement layers are nearly identical in appearance to those of insects, but have never been clearly identified. In addition, the structure of the inner epicuticle appears to be very peculiar because microfibre-like elements that are arranged in a twisted plywood structure are embedded in a matrix of medium electron density. Consequently, these structural peculiarities raise important questions about the chemical nature of the epicuticle layers of diplopods in relation to their roles in integument physiology and to their possible degree of homology or analogy to corresponding structures in other arthropods.

The main purpose of this study was to determine the chemical nature of the epicuticle components in the tergites of *G. marginata,* using cytochemical methods for the ultrastructural demonstration of chitin, proteins, and lipids. The results are discussed with special reference to the identity of the layers, their role in waterproofing or cuticle hardening, and their comparison with the cuticles of terrestrial and aquatic arthropods.

MATERIAL AND METHODS

Individuals of *Glomeris marginata* (Villers) were collected on the University campus of the Sart Tilman, Liège. To demonstrate chitin, ultrathin sections of glutaraldehyde-fixed, EDTA-decalcified and epoxy-resin-embedded tergites were incubated for 45 min on drops of a WGA-BSA-gold complex (wheat germ agglutinin, Sigma) in 0.02 M Na-phosphate buffer, pH 7.2 containing 0.5% BSA (HORISBERGER & ROSSET, 1977).

Tannic acid in the fixative medium was used as an indicative reagent for proteins (Hayat, 1993). EDTA-demineralised tergites were first fixed for 2 h at 20°C in a mixture of 1% tannic acid and 2.5% glutaraldehyde in 0.1 M Na-phosphate buffer pH 7.4, followed by a 72-hours incubation in 1% tannic acid. Protein-bound tannic acid was then revealed by "en bloc" uranyl acetate staining.

Two methods based on the reduction of OsO_4 were used to demonstrate lipids. The first was to increase the specificity of OsO_4 for unsaturated bonds in lipids under controlled experimental conditions (WIGGLESWORTH, 1981) and blocking reactions. Prior to staining (1 h at 20°C in 1% OsO_4 in 0.1 M Na-phosphate buffer, pH 7.4) the glutaraldehyde-fixed and EDTA-demineralised samples were treated for 4 h at 37°C in 1.25% N-ethylmaleimide-buffered solution for blocking sulfhydryl groups (GABE, 1968), then for 16 h at 20°C in nitrous acid (LILLIE, 1954 *in* GABE, 1968) or for 72 h in 2.5% glutaraldehyde fixative solution for blocking primary amines and then for 1 h at 60°C in saturated bromine water for blocking unsaturated bonds (MUKHERJI *et al.*, 1960). Free and bound lipids were distinguished after extraction of free lipids from glutaraldehyde-fixed material in a hot chloroform/methanol mixture.

The second method was detection of hydrophobic substances. A highly unsaturated lipid-soluble marker, myrcene, was incorporated by partition in 50% ethanol, then revealed by reduction of OsO_4 (WIGGLESWORTH, 1981). This treatment was performed after bromination.

Source : MNHN, Paris

RESULTS

The WGA-BSA-gold complex which is used to demonstrate chitin labels the microfibres in the procuticle and inner epicuticle (Fig. 2). In both layers, labelling depends on microfibre orientation as determined by the twisted plywood arrangement of the microfibres. The gold particles are distributed only along successive horizontal bands where the microfibres are seen in oblique section and are absent where the fibres appear in longitudinal section.

The method used to demonstrate proteins, tannic acid treatment followed by "en bloc" uranyl acetate staining, strongly enhances the electron density of the whole procuticle and of the cement layer, the cuticulin layer, and the inner epicuticle (Figs 3 & 4). In contrast, the wax layer remains completely electron-lucent. In the inner epicuticle, electron-dense rod-shaped elements are prominent against the electron lucent material of the matrix. As observed after classical staining (Fig. 1), these elements are oriented parallel to the microfibres.

The first method of lipid demonstration reveals unsaturated lipids in different epicuticular layers and shows that they are insoluble in organic solvents (Figs 5 & 6). The lipids are mainly located in the wax layer but also impregnate the cement layer and the upper leaflet of the cuticulin layer, both of which appear as intensely electron-dense borders. The moderate electron density of the lower leaflet of the cuticulin layer and inner epicuticle indicates that these layers are relatively poor in such lipids. As a control, oxidation of double bonds by bromination prior to OsO_4 staining prevents any osmiophilic reaction in the wax layer but merely reduces the contrast in the other epicuticular layers (Fig. 7). This remaining osmiophily is probably due to the presence of proteins. The presence of lipids in the epicuticular layers of *G. marginata* is confirmed by the results of the second procedure for detecting hydrophobic substances. Incorporation of myrcene after bromination and before OsO_4 staining restores a high electron density in the previously osmiophilic layers, i.e. the cement layer, the wax layer, and the upper leaflet of the cuticulin layer (Figs 8 & 9). However, it only slightly enhances the contrast of the lower leaflet of the cuticulin layer and the matrix material of the inner epicuticle, which seem to consist of lipoproteins. In contrast, the rod-shaped protein elements and the chitin microfibres remain electron-lucent.

DISCUSSION

The present cytochemical results combined with the previous ultrastructural observations of ANSENNE *et al.* (1990) allow accurate identification of the structural components of *Glomeris marginata* tergite epicuticle. Furthermore, considering the respective structures, chemical compositions, and roles of its constituents, the cuticle of *G. marginata* is consistent with the functional model recently proposed by COMPÈRE & GOFFINET (1992) for decapod crustaceans. According to this model, the cuticle includes two functional parts: the upper part is responsible of the integument permeability characteristics while the lower part contributes to the mechanical resistance of the exoskeleton. In *G. marginata,* the upper part includes the three outer epicuticular layers, i.e. the cement layer, the wax layer, and the cuticulin layer. The cement and wax layers can be regarded as integument adaptations to a terrestrial mode of life and as structures homologous to the corresponding layers of insect and arachnid cuticles (NEVILLE, 1975; FILSHIE, 1976; HADLEY, 1986). This view is strongly supported by their structure, location, chemical composition, and role in cuticular waterproofing in addition to the fact that the cement layer of *G. marginata* is discharged on the cuticular surface by dermal gland ducts (ANSENNE *et al.*, 1990), similar as in insects.

Since it labels both protein- and lipid-positive, the cement layer appears as an outer protection layer made of wax-impregnated proteins. Overlying the cuticulin layer, the wax layer consists exclusively of stabilized lipid compounds, most of them unsaturated. Similar solvent-resistant waxes have been reported for some insects (WIGGLESWORTH, 1985), for some arachnids (HADLEY, 1981), and for the diplopod *Orthoporus ornatus* (Girard) (WALKER &

Source : MNHN, Paris

CRAWFORD, 1980). More recently, the presence of a strongly osmiophilic wax layer was also described in *Ophyiulus pilosus* (Newport) (THOREZ *et al.*, 1992). The higher resistance of *G. marginata* to a dry environment compared to the poor water resistance of the isopod *Oniscus asellus* (L.) (EDNEY, 1951), could be ascribed to the absence of this layer in *O. asellus*, which only possesses free lipids inside the cuticulin layer instead of a distinct outer wax layer (COMPÈRE, 1990).

Although the accurate identification of the cuticulin layer components is still lacking, the present observations combined with those of ANSENNE *et al.* (1990) strongly suggest that the structure of this layer is comparable to that described for other arthropods (insects: LOCKE, 1966; arachnids: FILSHIE, 1976; crustaceans: COMPÈRE, 1988, 1990). The cuticulin layer of *G. marginata* exhibits a membrane-like structure approximately 20 nm thick which seems to consist of two protein leaflets, the upper one being impregnated with overlying waxes. These leaflets are separated by an electron-lucent layer probably made of lipid polymers, as suggested by the studies of WIGGLESWORTH (1985) and HACKMAN (1986) for insects and COMPÈRE & GOFFINET (1992) for the crab *Carcinus maenas* (L.). Appearing as a general arthropodian feature, the cuticulin layer can be regarded as a primitive structure, since it already constitutes the main permeability barrier of the cuticle in marine crustaceans (COMPÈRE & GOFFINET, 1992).

The inner epicuticle and procuticle are layers of the lower part which probably contribute to the mechanical properties of the cuticle. The inner epicuticle consists of a lipoprotein matrix surrounding proteinaceous rod-shaped elements and chitin-protein microfibres that prolong the helicoidal twisted plywood arrangement of the exocuticle fibres. This organisation appears very peculiar, never having been reported before in any other arthropod cuticle. The presence of chitin-protein fibres contradicts the first and classical definition of the insect epicuticle as a non-chitinous layer (KÜHNELT, 1928a,b). Considering that the inner epicuticle of the soft intersegmental regions of *G. marginata* (COMPÈRE, unpublished results) is composed, as in insect tergites (LOCKE, 1969; NEVILLE, 1975), of a homogeneous fibreless matrix, the thick inner epicuticle of the mineralised tergites of *G. marginata* can be interpreted as a result of close interpenetration between the epicuticular matrix material and the chitin-protein fibres of the exocuticle. Functionally, it can be regarded as a structure convergent with the inner epicuticle of decapod crustaceans, in addition to other features such as the pseudo-reticulate pattern of the exocuticle and mineralisation of the procuticle (ANSENNE *et al.*, 1990). As proposed by COMPÈRE & GOFFINET (1992) for the crab *C. maenas*, the thick fibrous inner epicuticle bearing roots on its lower side ensures mechanical reinforcement, preventing the upper layers and the mineralised exocuticle from splitting off.

FIG. 1. — Transverse section through the tergite epicuticle of *Glomeris marginata* after classical tissue fixation and uranyl acetate/lead citrate section staining. c, cuticulin layer; ct, cement layer; ie, inner epicuticle; rs, rod-shaped elements; w, wax layer;

➤, cross-sectioned chitin-protein microfibres; ❍/≡/⊗, microfibre orientation. Bar 5 µm.

FIG. 2. —Transverse section of the tergite epicuticle of *Glomeris marginata* after incubation with the WGA-BSA-gold complex and stained in uranyl acetate. ex, exocuticle; ie, inner epicuticle; ❍/≡/⊗, fibre orientation. Bar 0.5 µm.

FIGS 3 & 4. — Detail of the upper epicuticular layers after "en bloc" uranyl acetate staining (FIG. 4) and after exposure to tannic acid prior to "en bloc" uranyl acetate staining (FIG. 3). c, cuticulin layer; ct, cement layer; ie, inner epicuticle; rs, rod-shaped elements; w, wax layer. Bars 250 nm.

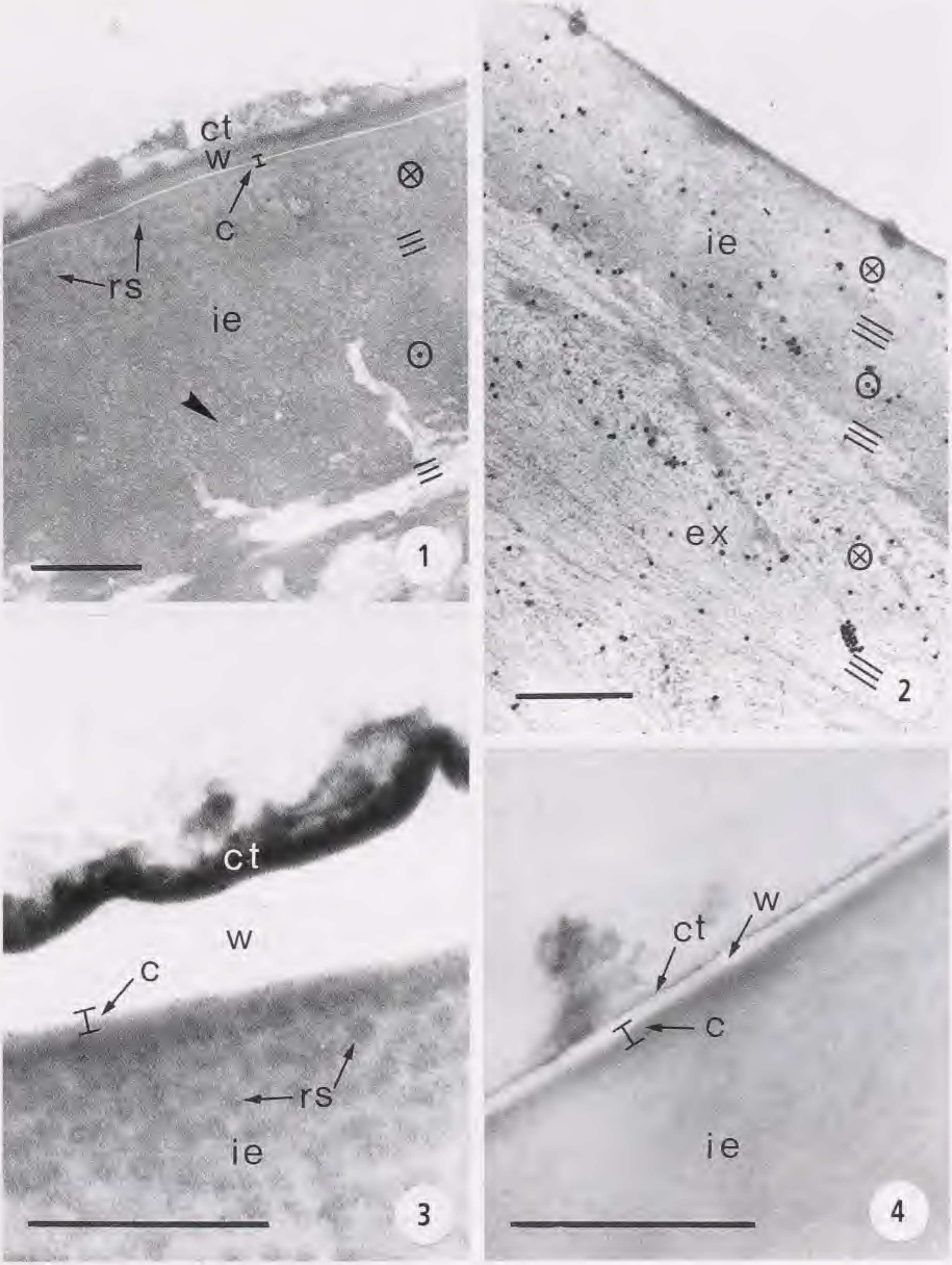
FIGS 5-9. — Vertical sections of the tergite epicuticle of *Glomeris marginata* after different cytochemical treatments. c, cuticulin layer; ct, cement layer; ex, exocuticle; ie, inner epicuticle; rs, rod-shaped elements; w, wax layer.

FIGS 5-6. After extraction of free lipids in a chloroform/methanol mixture, long fixation in buffered 2.5% glutaraldehyde and OsO_4 staining. Fig 5. Bar 1 µm. FIG. 6. Detail of the upper epicuticular layers. Bar 250 nm.

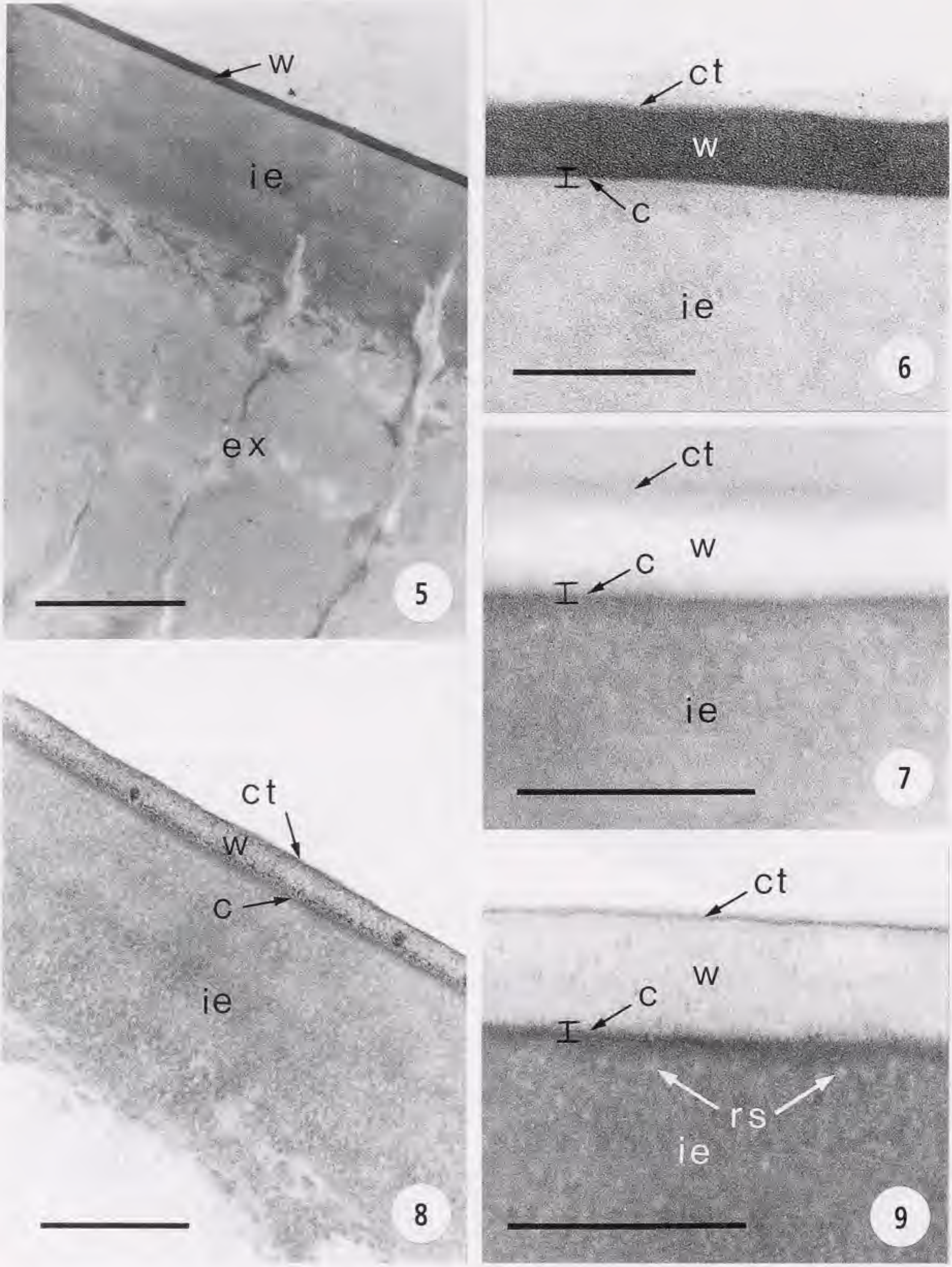
FIG. 7. Detail of the upper epicuticular layers after extraction of free lipids in a chloroform/methanol mixture, incubation in bromine water and OsO_4 staining. Bar 250 nm.

FIGS 8-9.— After extraction of free lipids in a chloroform/methanol mixture, incubation in bromine water, exposure to myrcene and OsO_4 staining. FIG. 8. Bar 1 µm. FIG. 9. Detail of the upper epicuticular layers. Bar 250 nm.

Source : MNHN, Paris



Source : MNHN, Paris



Source : MNHN, Paris

CONCLUSION

In conclusion, the present study sheds some light upon the relationships between the different cuticle layers in diplopods, their role in integumental physiology, and their ecological significance. In addition, our evidence supports the dual-function model of the cuticle, recently defined by COMPÈRE & GOFFINET (1992) for a marine decapod crustacean. This model also agrees with previous observations made on the cuticle of insects and arachnids (for reviews, see: NEVILLE, 1975; HADLEY, 1981, 1984, 1986), we tentatively propose it as more general for arthropod cuticular structure.

ACKOWNLEDGEMENTS

The authors are indebted to the Belgian Fund for Joint Basic Research for its financial support of this work (F.R.F.C., convention N°2.4527.89). P.C. is the recipient of a grant from the National Fund for Scientific Research (F.N.R.S., Belgium).

REFERENCES

ANSENNE, A., COMPERE , P. & GOFFINET, G., 1990. — Ultrastructural organization and chemical composition of the mineralized cuticle of *Glomeris marginata* (Myriapoda, Diplopoda). *In* : A. MINELLI, *Proc. 7th Intern. Congr. of Myriapodology.*, Leiden, Brill : 125-134.

COMPERE, P., 1988. — Mise en place de l'épicuticule chez le crabe *Carcinus maenas.* Aspects récents de la Biologie des Crustacés, *Actes de Colloques IFREMER*, **8** : 47-54.

COMPERE, P., 1990. — Fine structure and elaboration of the epicuticule and pore canal system in tergite cuticle of the land isopod *Oniscus asellus* during a molting cycle. *In* : P. JUCHAULT & J. P. MOCQUARD, *Biology of terrestrial Isopods III, Proc. 3rd Int. Symp. Biology terrestrial Isopods*, Poitiers : 169-175.

COMPERE, P. & GOFFINET, G., 1992. — Organisation tridimensionnelle et cytochimie de l'épicuticule et des systèmes canaliculaires des sclérites du crabe *Carcinus maenas* (Crustacé décapode). *Mém. Soc. r. belge Ent.*, **35** : 715-720.

EDNEY, E. B., 1951. — The evaporation of water from woolice and the millipede *Glomeris. J. exp. Biol.*, **28** : 91-115.

FILSHIE, B. K., 1976. — The structure and deposition of the epicuticle of the adult female cattle tick (*Boophilus microplus*). *In* : H. R. HEPBURN, *The Insect Integument*, Amsterdam, Elsevier : 193-206.

GABE, M., 1968. — *Techniques histologiques.* Paris, Masson, 1113 pp.

HACKMAN, R. H., 1986. — The chemical nature of the outer epicuticle from *Lucilia cuprina* larvae. *Insect Biochem.*, **16** : 911-916.

HADLEY, N. F., 1981. — Cuticular lipids of terrestrial plants and Arthropods: a comparison of their structure, composition and waterproofing function. *Biological Rev.*, **56** : 23-47.

HADLEY, N. F., 1984. — Arthropoda : Cuticle : Ecological Signifiance. *In* : BEREITER-HAHN, A. G. MATOLTSY & K. S. RICHARDS, *Biology of the Integument, 1. Invertebrates*, Berlin, Springer Verlag : 685-693.

HADLEY, N. F., 1986. — La cuticule des Arthropodes. *Pour la Science*, **107** : 64-72.

HAYAT, M. A., 1993. — *Stains and cytochemical methods.* Plenum Publ. Corp., New York, London, 445 pp.

HORISBERGER, M. & ROSSET, J., 1977. — Colloidal gold, a useful marker for transmission and scanning electron microscopy. *J. Histochem. Cytochem.*, **25** : 295-305.

KÜHNELT, W., 1928a. — Ein Beitrag zur Histochemie des Insektenskelettes. *Zool. Anz.*, **75** : 111-115.

KÜHNELT, W., 1928b. — Studien über den mikrochemischen Nachweis des Chitins. *Biol. Zentralbl.*, **48** : 374-382.

LOCKE, M., 1966. — The structure and formation of the cuticulin layer in the epicuticle of an insect, *Calpodes ethlius* (Lepidoptera, Hesperiidae). *J. Morph.*, **118** : 416-494.

LOCKE, M., 1969. — The structure of epidermal cells during the development of the protein epicuticle and uptake of molting fluid in an Insect. *J. Morph.*, **127** : 7-40.

MUKHERJI, M., DEB, C. & SEN, P. B.,1960. — Histochemical demonstration of unsaturated lipids by bromine silver method. *J. Histochem. Cytochem.*, **8** : 189.

NEVILLE, A. C., 1975. — Biology of the arthropod cuticle. *In* : W. S. HOAR, J. JACOBS, H. LANGER & M. LINDAUER, *Zoophysiology and Ecology, Vol. 4/5*, Berlin, Springer Verlag, 448 pp.

THOREZ, A., COMPERE, P. & GOFFINET, G., 1992. — Ultrastructure and mineral composition of the tergite cuticle of the iulid millipede *Ophyiulus pilosus* (Myriapoda, Diplopoda). *Ber. nat.-med. Verein Innsbruck,* **suppl. 10** : 63-69.

WALKER, L. J. & CRAWFORD, C. S., 1980. — Integumental ultrastructure of the desert millipede, *Orthoporus ornatus* (Girard) (Diplopoda : Spirostreptidae). *Int. J. Insect Morphol. Embryol.*, **9** : 231-249.

WIGGLESWORTH, V. B., 1981. — The distribution of lipid in the cell structure: an improved method for the electron microscope. *Tissue Cell*, **13** : 19-34.

WIGGLESWORTH, V. B., 1985. — Sclerotin and lipid in the waterproofing of the insect cuticle. *Tissue Cell*, **17** : 227-248.

Source : MNHN, Paris

Source : MNHN, Paris

Coxal Organs of Chilopoda: the Exocrine Glands in *Lithobius forficatus*

Jörg ROSENBERG * & *Hartmut* GREVEN **

* Institut für Tierphysiologie, Fakultät für Biologie, Ruhr-Universität Bochum, D-44780 Bochum, Germany
** Institut für Zoologie (Zoomorphologie und Zellbiologie) der Heinrich-Heine-Universität-Düsseldorf
Universitätsstraße 1, D-40225 Düsseldorf, Germany

ABSTRACT

The exocrine glands within the coxal organs of *Lithobius forficatus* are described. Each gland consists of secretory cells, an additional cell and a canal cell, forming a cuticular ductule (class 3 gland according to NOIROT & QUENNEDY, 1974). Secretory cells are rich in rER and PA-TCH-SP (periodic acid-thiocarbohydrazide-silver proteinate)-positive secretory granules. The additional or intercalary cells possess numerous mitochondria and prominent infoldings of the plasma membrane beneath the cuticle of the transport duct. PA-TCH-SP-positive secretory products are obviously discharged along the cuticular ductule into the pore channel of the coxal organ, forming a mucous layer that covers the specialized cuticle of the transport epithelium. Within its subcuticle, chloride can be localized cytochemically; its accumulation in the mucous layer is not significant.

RÉSUMÉ

Organes coxaux des Chilopodes : les glandes exocrines de *Lithobius forficatus*.

Les glandes exocrines des organes coxaux de *Lithobius forficatus* sont décrites. Chaque glande est composée de cellules sécrétrices, d'une cellule additionnelle et d'une cellule-canal, constituant un canalicule cuticulaire [glande de classe 3 selon NOIROT & QUENNEDY (1974)]. Les cellules sécrétrices sont riches en rER et en PA-TCH-SP ("periodic acid-thiocarbohydrazide-silver proteinate") sous forme de granules de sécrétion. Les cellules additionnelles ou intercalaires possèdent de nombreuses mitochondries et des protubérances en doigts de gant de la membrane du plasma en dessous de la cuticule du canalicule. Les produits sécrétés (PA-TCH-SP-positif) sont évacués le long du conduit cuticulaire jusqu'au pore de l'organe coxal, formant une couche de mucus qui couvre la cuticule spécialisée de l'épithélium de transport. A l'intérieur de sa sous-cuticule, les chlorures peuvent être localisés cytochimiquement ; leur accumulation dans la couche de mucus n'est pas significative.

INTRODUCTION

Coxal organs of Chilopoda are complex and possibly multifunctional structures. They are localized on the coxae of the last trunk segment (Geophilomorpha, Scolopendromorpha) or last four trunk segments (Lithobiomorpha) and characterized by numerous pores, each leading into a cuticle-lined pore channel surrounded by a columnar single-layered transport epithelium and - arranged like a collar - junctional cells and several exocrine glands pouring out their secretory products into the lumen of the pore channel. This secretion covers the specialized cuticle of the transport epithelium (for review see ROSENBERG, 1985).

ROSENBERG, J. & GREVEN, H., 1996. — Coxal organs of Chilopoda: the exocrine glands in *Lithobius forficatus*. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 403-409. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

The general ultrastructure of the coxal organs in Chilopoda (ROSENBERG, 1982, 1983a, b, 1984, 1990) and also in experimental studies, particularly those on *Lithobius forficatus*, suggest that they are involved in water vapour uptake from the environment (ROSENBERG, 1985; ROSENBERG & BAJORAT, 1984). More recently, some evidence has been accumulated suggesting that coxal organs of Lithobiomorpha release a sex-specific pheromone (LITTLEWOOD, 1988, 1991; LITTLEWOOD & BLOWER, 1987). The authors speculate that sub-epithelial blood cells beneath the coxal organs might synthesize this pheromone, which moves across the epithelium of the coxal organ. These assumptions prompted us to examine the "glandular system" of the coxal organs, especially as recent investigations have revealed numerous small epidermal glands close to the coxal pores (ROSENBERG, 1994). On principle such structures could act as pheromone glands.

The following note deals with the exocrine glands of the coxal organs in *Lithobius forficatus* which were not described by LITTLEWOOD (1983) in Lithobiomorpha.

MATERIALS AND METHODS

Coxae of adult *Lithobius forficatus* were fixed as described previously (ROSENBERG 1983a). For detecting "mucosubstances", animals were fixed with 2.5% glutar dialdehyde and 2% formaldehyde (freshly prepared from paraformaldehyde) in phosphate buffer without any postfixation. After graded ethanol dehydration, tissue was embedded in LR White (London Resin Co.). Ultrathin sections were mounted on formvar-coated Ni grids. The periodic acid-thiocarbohydrazide-silver proteinate (PA-TCH-SP) reaction was performed as described by NEISS (1988). The sections remained unstained.

For demonstration of chloride the coxae were fixed according to WICHARD & KOMNICK (1973) with osmium tetroxide and silver lactate and treated with nitric acid during dehydration.

Sections were examined in a Zeiss 109 T electron microscope.

RESULTS

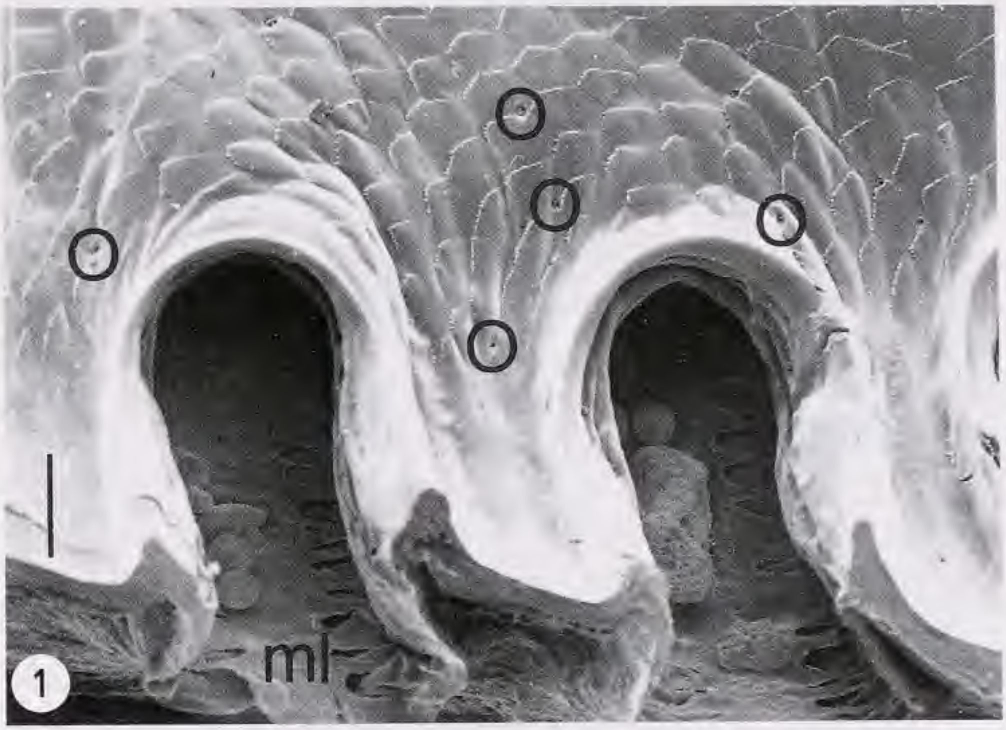
The topography of the exocrine glands within the coxal organs of *Lithobius forficatus* has been described elsewhere (ROSENBERG, 1983a, 1985). Each exocrine gland consists of three types of cells: secretory cells with well-developed granular ER, an additional or intercalary cell, forming microvilli-like projections surrounding a cuticular ductule, and a canal cell, whose cuticular duct runs into the pore channel (Figs 1 & 5).

The secretory cells are spheroidal or spindle-shaped. Their plasma membrane is moderately infolded. Cells are connected with adjacent additional cells by septate desmosomes. The cytoplasm of most secretory cells is packed with stacks of granular endoplasmic reticulum, which is filled with a fineley particulate substance (Fig. 3). In addition, these cells contain numerous dictyosomes in different stages of development and numerous electron dense secretory granules, which are membrane bounded and vary widely in size. Small mitochondria, and some lysosomes and multivesicular bodies, are distributed randomly throughout the cytoplasm. Each secretory cell has a large, lobate nucleus; its chromatin is mostly located peripherally. The thin cuticular ductule of the secretory cell is continuous with the wall of the transport duct of the additional cell.

PA-TCH-SP reaction reveals precipitations at the margins of secretory granules and in some profiles, derived from endoplasmic reticulum (Fig. 6).

The additional duct forming cell is more elongated and its cytoplasm is lighter than that of the secretory cells or adjacent cells of the transport epithelium. Large profiles of endoplasmic reticulum and dictyosomes are absent, and the small nucleus is oval. The plasma membrane surrounding the cuticular duct is folded forming long microvilli-like projections (Fig. 4). Mitochondria are numerous along the apical infoldings, they are larger than in the secretory cell. The wall of the cuticular duct is continuous with the cuticle of the small canal cell and that of the epicuticle of the pore channel of the coxal organ (Fig. 5). As seen by SEM (Fig. 2) and TEM (Fig. 1), secretion is deposited as a distinct mucous layer on the cuticle of the transport epithelium.

Source : MNHN, Paris



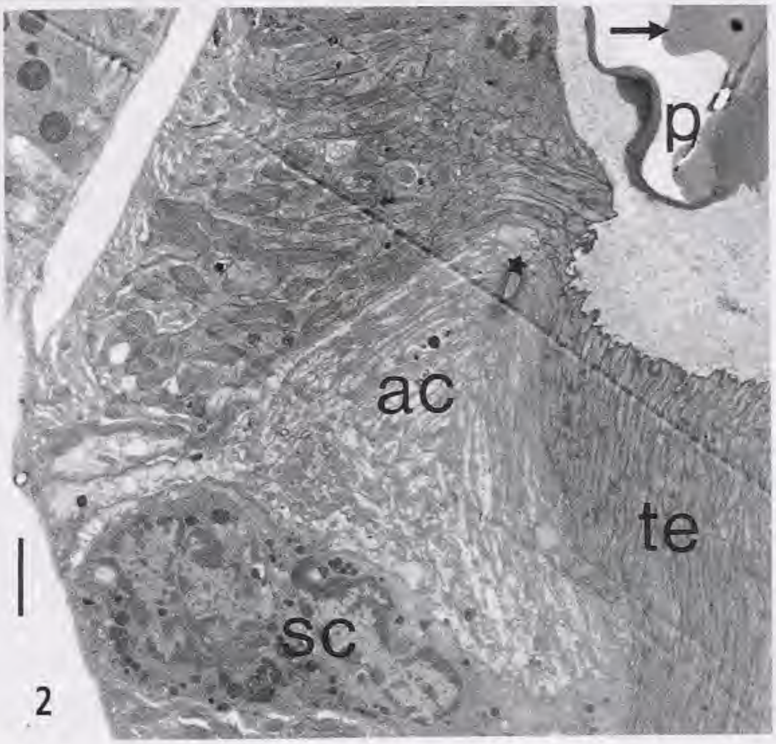
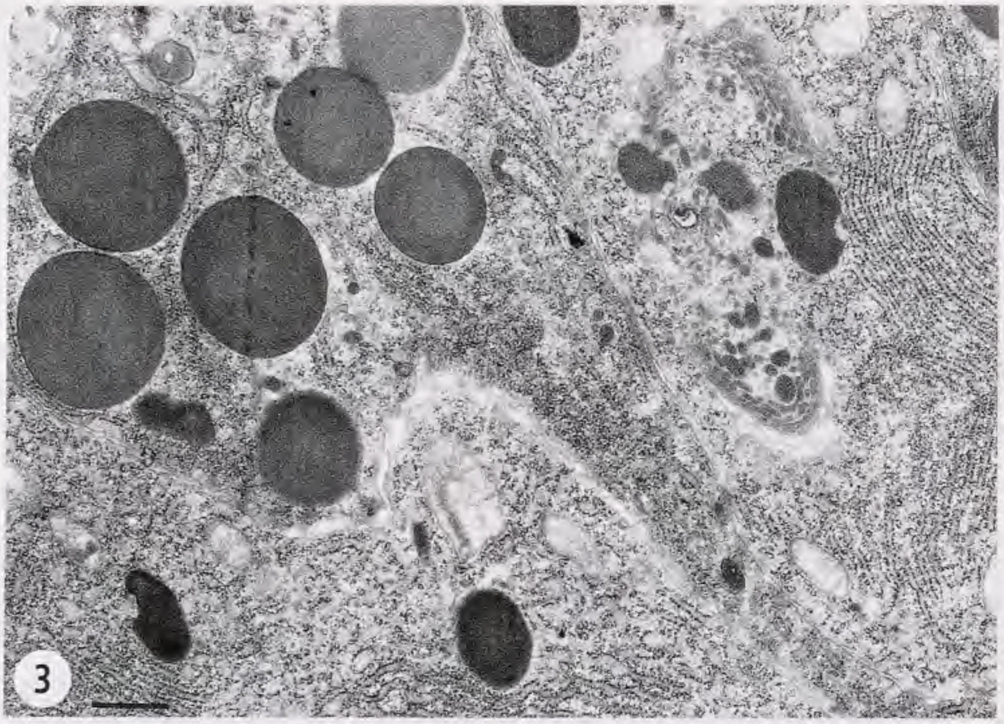


FIG. 1. — Section of two coxal pores of *Lithobius forficatus*, showing the mucous layer (ml) on the bottom of the pore channel and several openings of epidermal glands (circles) around the coxal pores. Scale line, 20 µm.

FIG. 2. — Part of the coxal organ of *Lithobius forficatus* with the transport epithelium (te) and its specialized cuticle, covered by the mucous layer (arrow), and the exocrine gland with secretory cells (sc) and an additional cell (ac) with its cuticular duct (*). p pore channel. Scale line, 0.08 µm.

Source : MNHN, Paris



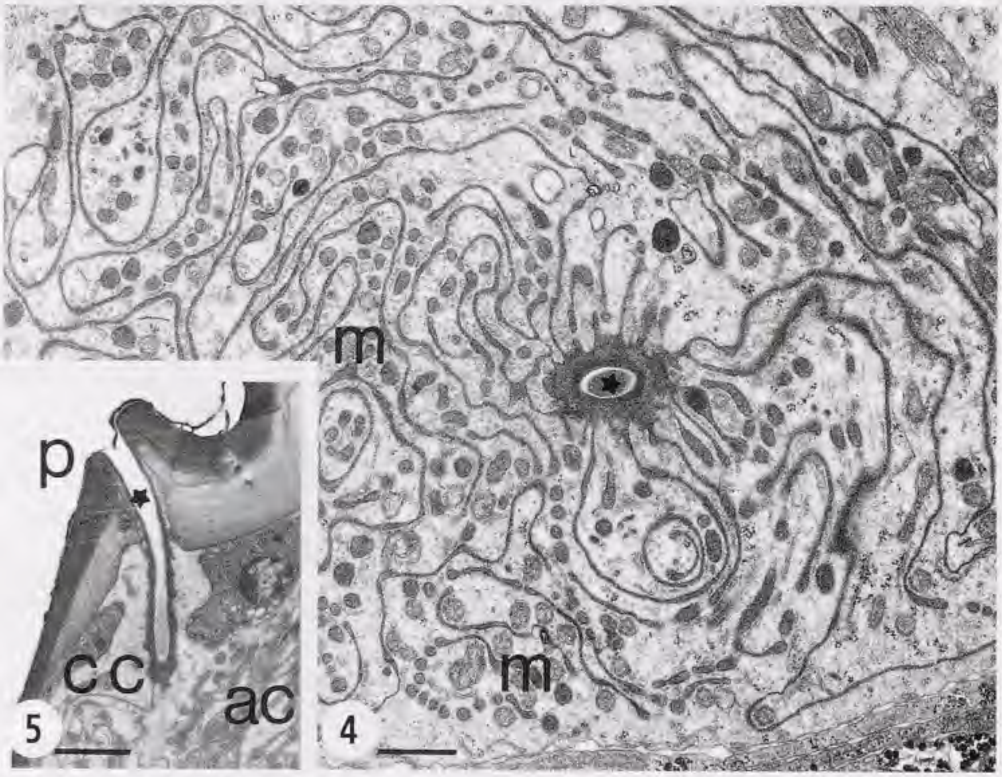


FIG. 3. — Secretory cells of the exocrine gland of the coxal organ with stacks of ER, dictyosomes, and secretory products. Scale line, 0.08 µm.

FIG. 4. — Additional cell of the exocrine gland of the coxal organ. The cuticular ductule (*) is surrounded by infoldings of the apical plasma membrane. m: mitochondrium. Scale line, 0.08 µm.

FIG. 5. — Additional cell (ac) and canal cell (cc) of the exocrine gland of the coxal organ. Their cuticular ductule (*) opens into the pore channel (p) of the coxal organ. Scale line, 0.1 µm.

Source : MNHN, Paris

Within the accessory cells (intercalary and canal cell), treatment by PA-TCH-SP stains the content of the transport duct, its cuticle, the material underlying the cuticle of the duct and the space between the microvilli-like projections (Fig. 7). A positive reaction is also seen in the mucous layer, covering the modified cuticle of the main epithelium (Fig. 8).

In coxal organs, fixed in the osmium-silver-lactate mixture, coarse precipitates are localized predominantly in the subcuticle of the specialized cuticle, covering the transport epithelium (Fig. 9). Fine precipitations seem to be scattered within the overlying endocuticle and in the mucous layer (Fig. 10). No precipitates are found within the cells of the transport epithelium, within the cuticle of the pore channel (Fig. 9), or within the cells of the exocrine gland.

DISCUSSION

The exocrine glands described for the coxal organs of *Lithobius forficatus* can be characterized as "class 3 glands" according to NOIROT & QUENNEDY (1974). In a simple case "a cuticular ductule or canal penetrates the gland cell and the canal runs into a ductule or canal cell which has secreted it" (p. 63). Within the exocrine glands of *Lithobius forficatus*, this description is complicated by the presence of an additional or intercalary cell between the two others. In *Lithobius forficatus* "class 3 glands" appear to be common; they are known to be present adjacent to the telopodal glands and are associated with sensilla trichodea (KEIL, 1975) as well as with the organs of Tömösvary (TICHY, 1973). It is assumed that these glands, although similar in organization, produce substances of different chemical composition and significance.

Considering the ultrastructure of secretory cells, in particular the abundant rough endoplasmic reticulum and the electron dense granules, there is reason to believe that secretory products contain a considerable amount of proteins. However, well-developed dictyosomes and the positive reaction after PA-TCH-SP are indicative of a carbohydrate component ("mucosubstances"). PA-TCH-SP positive material has also been demonstrated within the transport ductule and the mucous layer covering the specialized cuticle of the transport epithelium.

Location of the exocrine glands suggests discharge of secretory products through transport ductules into the pore channel of the coxal organ. As seen by SEM and TEM, the secretion spreads over the modified cuticle of the transport epithelium (LITTLEWOOD, 1983; ROSENBERG, 1983a) and fills up the bottom of the pore channel. Material that is electron-dense to varying degrees, interpreted as the mucous layer, has been observed in all coxal organs hitherto examined (ROSENBERG, 1985). It stains with PA-TCH-SP in *Lithobius forficatus* , but also in *Cryptops hortensis* (Scolopendromorpha; ROSENBERG, 1983b). It was suggested that this mucus consists of a hygroscopic material, which would gather water vapour from moist air (ROSENBERG, 1983a, 1985; ROSENBERG & BAJORAT, 1984).

Apart from forming the transport ductule, the role of the additional cell is unclear. Enlarged surfaces and abundant mitochondria in these cells suggest transporting ability, perhaps to modify secretion products within the ductule.

Localization of chloride in the modified cuticle of the coxal organ has been regarded as an indication of transepithelial solute transport as it is in the "chloride cells" of other transporting systems (e.g. anal papillae, anal organs, ventral tube, coxal vesicles) in a variety of insects (WICHARD & KOMNICK, 1973; KOMNICK, 1977; EISENBEIS, 1976; EISENBEIS & WICHARD, 1975). Accumulation in the mucous layer, however, seems not to be significant.

In general, the results presented here neither contradict the assumed uptake of water vapour from the air by coxal organs nor the pheromone release. However, there is still no definite proof for a hygroscopic capacity of the mucous layer; the epidermal glands close to the coxal pores are the presumed site of pheromone production (ROSENBERG, 1994).

Source : MNHN, Paris

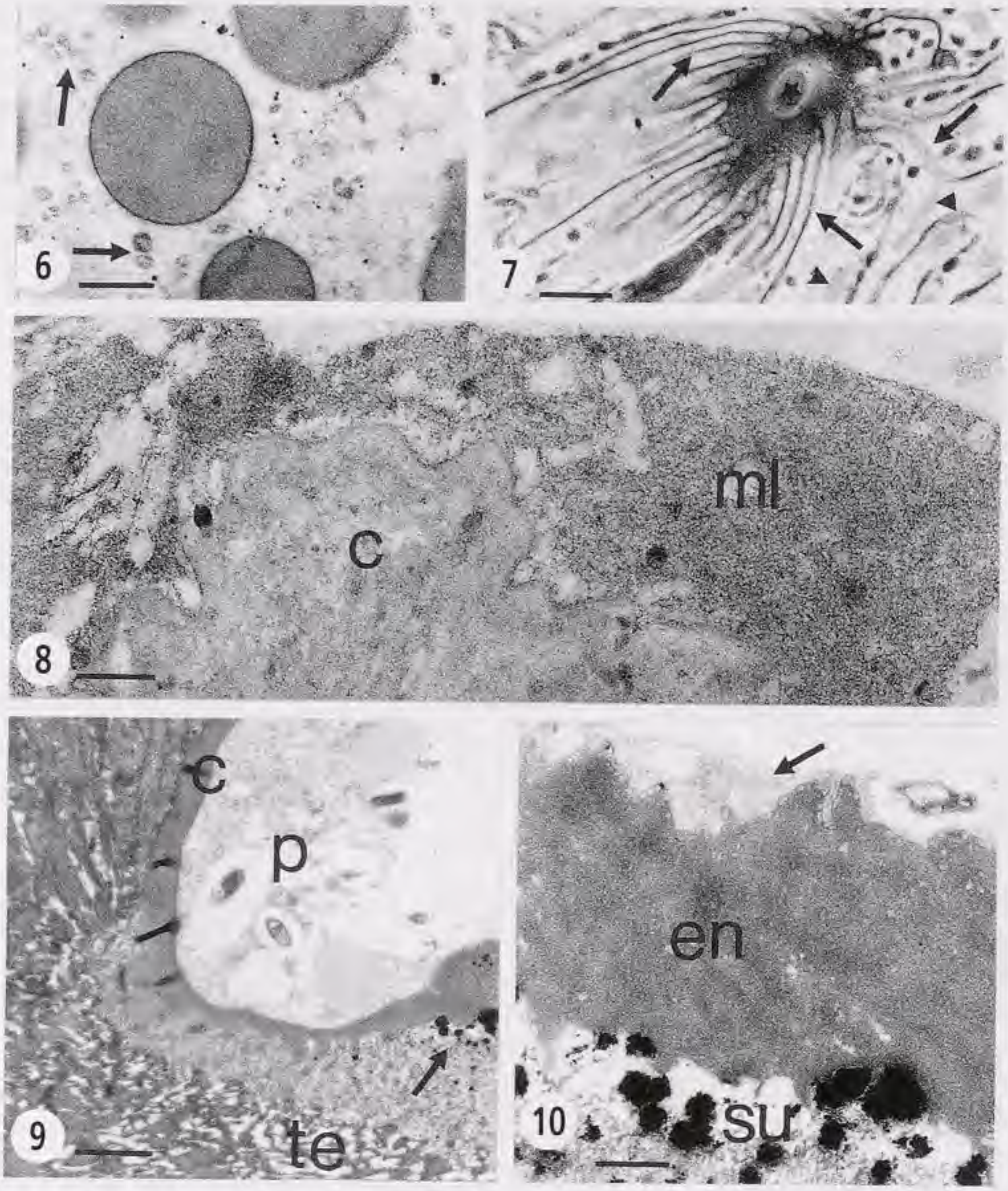


FIG. 6. — PA-TCH-SP-reaction in secretory cells (unstained sections): reaction products are visible at the margin of the secretory granules and in profiles of the ER (arrow). Scale line, 0.04 µm.

FIG. 7. — PA-TCH-SP-reaction in additional cell (unstained section): reaction products are visible within the cuticular duct (*) and the space underlying the duct, and between the microvillar infoldings (arrows). Mitochondrium (arrowhead). Scale line, 0.05 µm.

FIG. 8. — PA-TCH-SP-reaction in mucous layer (unstained section): the reaction products are only visible within the mucous layer (ml). C cuticle of the transport epithelium. Scale line, 0.03 µm.

FIG. 9. — Chloride-reaction in cuticle of the transport epithelium: a part of the coxal organ is shown with the transport epithelium (te) and the cuticle (c) of the pore channel (p). Reaction products (arrow) are only visible within the subcuticle of the main epithelium. Scale line, 0.1 µm.

FIG. 10. — Chloride-reaction in cuticle of the transport epithelium: coarse reaction products are localized within the subcuticle (su); fine precipitations are scattered within the endocuticle (en) and in the mucous layer (arrow). Scale line, 0.03 µm.

Source : MNHN, Paris

ACKNOWLEDGMENTS

We would like to thank Mr. H. SCHLIERENKAMP for careful technical assistance.

REFERENCES

EISENBEIS, G., 1976. — Zur Feinstruktur und Histochemie des Transportepithels abdominaler Koxalblasen der Doppelschwanz-Art *Campodea staphylinus* (Diplura: Campodeidae). *Ent. Germ.*, **3** : 185-201.

EISENBEIS, G. & WICHARD, W., 1975. — Feinstruktureller und histochemischer Nachweis des Transportepithels am Ventraltubus symphypleoner Collembolen (Insecta, Collembola). *Z. Morph. Tiere*, **81** : 103-110.

KEIL, T., 1975. — Die Antennensinnes- und Hautdrüsenorgane von *Lithobius forficatus* (L.). Eine licht- und elektronenmikroskopische Untersuchung. Dissertation, University of Berlin.

KOMNICK, H., 1977. — Chloride cells and chloride epithelia of aquatic insects. *Int. Rev. Cytol.*, **49** : 285-327.

LITTLEWOOD, P. M. H., 1983. — Fine structure and formation of the coxal glands of Lithobiomorph centipedes: *Lithobius forficatus* (L.) and *Lithobius crassipes* Koch (Chilopoda, Lithobiomorpha). *J. Morphol.*, **177** : 157-180.

LITTLEWOOD, P. M. H., 1988. — The chemosensory behaviour of *Lithobius forficatus* (Myriapoda: Chilopoda). 2. Bioassay and chemistry of the coxal pheromone. *J. Zool., London* , **215** : 523-535.

LITTLEWOOD, P. M. H., 1991. — Chilopod coxal organs: morphological considerations with reference to function. *J. Zool., London* , **223** : 379-393.

LITTLEWOOD, P. M. H. & BLOWER, J. G., 1987. — The chemosensory behaviour of *Lithobius forficatus*. 1. Evidence for a pheromone released by the coxal organs (Myriapoda: Chilopoda). *J. Zool., London*, **211** : 65-82.

NEISS, W. F., 1988. — Enhancement of the periodic acid-Schiff (PAS) and periodic acid-thiocarbohydrazide-silver proteinate (PA-TCH-SP) reaction in LR White sections. *Histochemistry*, **88** : 603-612.

NOIROT, C. & QUENNEDEY, A., 1974. — Fine structure of insect epidermal glands. *Annual Rev. Entomology*, **19** : 61-80.

ROSENBERG, J., 1982. — Coxal organs in Geophilomorpha (Chilopoda). Organization and fine structure of the transporting epithelium. *Zoomorphology*, **100** : 107-120.

ROSENBERG, J., 1983a. — Coxal organs of *Lithobius forficatus* (Myriapoda, Chilopoda). Fine-structural investigation with special reference to the transport epithelium. *Cell Tiss. Res.*, **230** : 421-430.

ROSENBERG, J., 1983b. — Coxal organs in Scolopendromorpha (Chilopoda): Topography, organization, fine structure and signification in centipedes. *Zool. Jb. (Anat.)*, **110** : 383-393.

ROSENBERG, J., 1984. — Ultrastructure of the anal organs in the larval stages of *Lithobius forficatus* (L.) (Chilopoda: Lithobiomorpha). *Int. J. Insect Morph. Embryol.*, **13** : 29-35.

ROSENBERG, J., 1985. — Untersuchungen zur feinstrukturellen Organisation und Funktion der Coxalorgane und Analorgane bei Chilopoda. *Bijdr. Dierk.* , **55** : 181-189.

ROSENBERG, J., 1990. — Untersuchungen zur funktionellen Morphologie der Analorgane von Geophilidae (Geophilomorpha). *In* : A. MINELLI, *Proc. 7th. Intern. Congr. Myriapodology* . Leiden, Brill : 115-123.

ROSENBERG, J., 1994. — Fine structure of epidermal glands in vicinity to the coxal organs of *Lithobius forficatus* (Chilopoda). *Acta Biol. Benrodis*, **6** : 37-47.

ROSENBERG, J. & BAJORAT, K. H., 1984. — Einfluß der Coxalorgane von *Lithobius forficatus* (L.) (Chilopoda) auf die Sorption von Wasserdampf. *Zool. Jb. (Physiol.)* , **88** : 337-344.

TICHY, H., 1973. — Untersuchungen über die Feinstruktur des Tömösvaryschen Sinnesorgans von *Lithobius forficatus* (L.) (Chilopoda) und zur Frage seiner Funktion. *Zool. Jb. (Anat.)* , **91** : 93-139.

WICHARD, W. & KOMNICK, H., 1973. — Fine structure and function of the abdominal chloride epithelia in caddisfly larvae. *Z. Zellforsch.*, **136** : 579-590.

Source : MNHN, Paris

Source : MNHN, Paris

The Phenoloxidase from the Hemolymph of Diplopoda

Willi E. R. XYLANDER

Institut für Allgemeine und Spezielle Zoologie, Justus-Liebig-Universität Giessen
Stephanstr. 24, D - 35390 Giessen, Germany

ABSTRACT

The phenoloxidases of the diplopods *Chicobolus* sp. and *Rhăpidostreptus virgator* occur in the hemolymph as proenzyme, prophenoloxidase (proPO). It can be activated in vitro by incubation with ethanol or methanol whereas chymotrypsin only activates the proPO of *Rhapidostreptus*. Microbial substances have little effect on the proPO of both species. Dopa showed to be a good substrate, dopamine and pyrogallol were less, tyrosine and others hardly converted at all. Phenylthiourea is a potent inhibitor. The pH optimum was about pH7 in both species. In SDS-PAGE the proPO had a molecular weight of about 230 kDa in both species and in *Lithobius forficatus*. The proPO is located in the grana of the two types of granular hemocytes but not in the plasmatocytes. Microbial substances and other material (glass, sephadex, latex beads) did not induce exocytosis and activation of the proPO but it is activated during wound clot formation (as shown by melanisation of the clot). Thus the activation mechanism of this defence system is somewhat different from that of insects and crustaceans and may be involved in antimicrobial defence at wound margins.

RÉSUMÉ

La phénoloxydase de l'hémolymphe des diplopodes.

La phénoloxydase des diplopodes *Chicobolus* sp. et *Rhapidostreptus virgator* existe dans l'hémolymphe en tant que proenzyme de la phénoloxydase (proPO). Elle peut être activée *in vitro* par l'éthanol et le méthanol, tandis que la chymotrypsine active uniquement celle de *Rhapidostreptus*. Les substances microbiennes ont très peu d'effet sur les proPO des deux espèces. La dopa s'avère être un bon substrat, tandis que la dopamine et le pyrogallol le sont moins. En revanche, la tyrosine et d'autres substances ne sont pour ainsi dire pas métabolisées. La phénylthiourée convient parfaitement comme substance inhibitrice. La valeur optimale du pH est pH7. Dans le SDS-PAGE, la proPO des deux espèces, de même que celle de *Lithobius forficatus*, a un poids moléculaire d'environ 230 kDa. Elle est surtout localisée dans les grana des deux types d'hémocytes granulaires, mais elle manque dans les plasmocytes. Des substances microbiennes et d'autres matériaux (verre, grains de séphadex et de latex), ne provoquent pas l'exocytose des grana contenant la proPO mais sont activés pendant la cicatrisation (comme on peut le dépister dans la mélanisation). Apparemment, les mécanismes d'activation de ce système immunologique sont différents de ceux des insectes et des crustacés ; ils sont probablement impliqués dans la défense antimicrobienne qui se développe au bords des plaies.

INTRODUCTION

The phenoloxidase (PO) from the hemolymph of arthropods and the enzymes involved in its activation play an important role in immune defence responses. In many arthropods, they are stored in the hemocytes as inactive zymogen, the prophenoloxidase (proPO). Once set free by exocytosis the enzyme becomes "sticky" and attaches to the surface of foreign particles where the activation of the proPO and subsequent formation of melanin occurs (SÖDERHÄLL, 1982).

XYLANDER, W. E. R., 1996. — The Phenoloxidase from the hemolymph of Diplopoda. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 411-420. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

The immune defence reactions in which the hemolymph PO is involved comprise synthesis of bacteriostatic and fungicide intermediate products of melanin formation, opsonization, melanin deposition on the surfaces of metazoan and protozoan parasites, and wound closure (ASHIDA & YAMAZAKI, 1990; CHADWICK & ASTON, 1978; GÖTZ & VEY, 1974; PYE, 1974; RATCLIFFE *et al.*, 1984; VEY & GÖTZ, 1975). This paper presents the results of investigations on the hemolymph PO of two diplopods (*Rhapidostreptus virgator* and *Chicobolus* sp.).

MATERIAL AND METHODS

Two diplopods (*Chicobolus* sp. and *Rhapidostreptus virgator*) were reared and hemolymph was obtained following the description given by XYLANDER & NEVERMANN (1990). The methods of PO investigations in the in-vitro-system (see Fig. 1), the calculation of PO-activity and the preparation of SDS-PAGE under non-reducing conditions were described in detail by XYLANDER & BOGUSCH (1992). The procedure of demonstration of intracellular proPO in the hemocytes was presented by XYLANDER & NEVERMANN (1993).

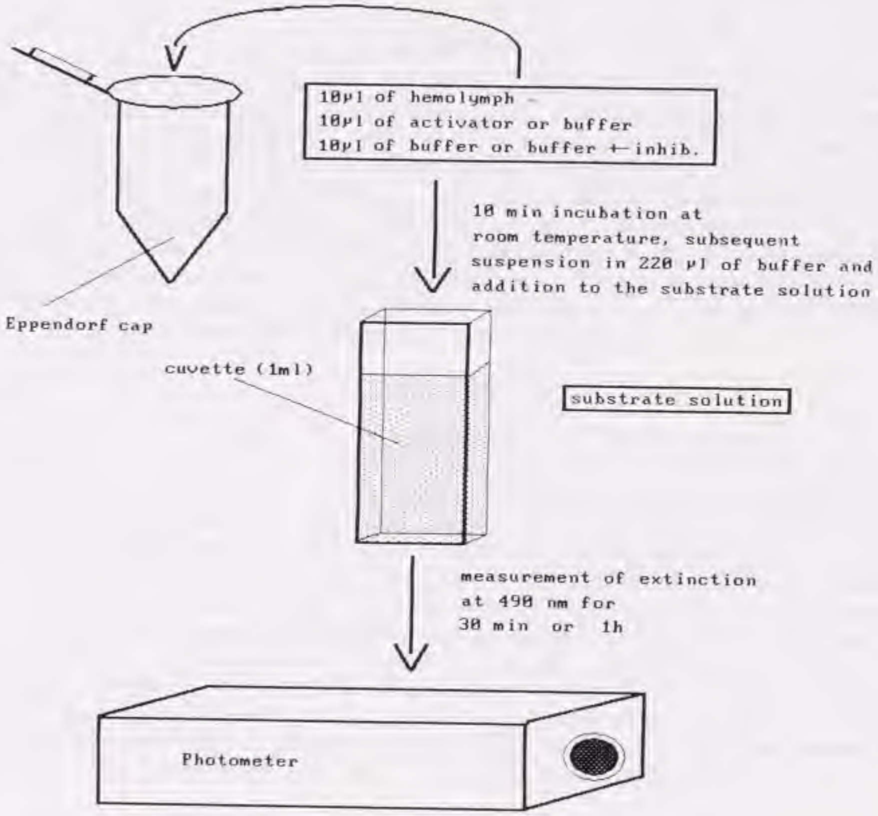


FIG. 1. — Procedure of in-vitro-measurement of PO activity.

RESULTS

In-vitro-activity

The in-vitro-activity of the phenoloxidase (PO) without any activator is comparatively low: 0.65 [ml^{-1} min^{-1}] in *Rhapidostreptus* (XYLANDER & BOGUSCH, 1992) and 0.133 [ml^{-1} min^{-1}] in *Chicobolus* (Fig. 2). This means that the PO occurs in the hemolymph as inactive zymogen, the prophenoloxidase (proPO). The level of PO-activity in the hemolymph depended on the season; it was generally higher in summer (during the main period of activity) than in winter.

Source : MNHN, Paris

The proPO can be activated by incubation of hemolymph with organic solvents (e. g. ethanol, methanol, SDS) and proteases (α-chymotrypsin) for 10 min; maximum activity (the highest activity measured) was generally higher in *Rhapidostreptus* than in *Chicobolus*, however, the relative increase in activity after activation (activity without activation = 1) was higher in *Chicobolus* (compare Figs 2 & 3). Ethanol is the best activator tested and raises the PO-activity 20times (in *Rhapidostreptus*) to 35times (in *Chicobolus*; A = 7.42; see Figs 2 & 3). Methanol is a less efficient activator than ethanol in both species. α-chymotrypsin is a good activator in *Rhapidostreptus* but shows only little effect in *Chicobolus* (Figs 2 & 3).

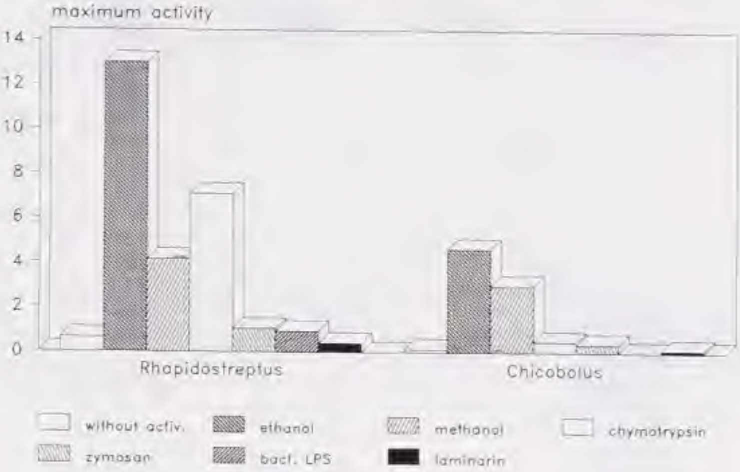


FIG. 2. — Absolute in-vitro-activity of the hemolymph of *Rhapidostreptus virgator* and *Chicobolus* sp. without and with application of various potential activators.

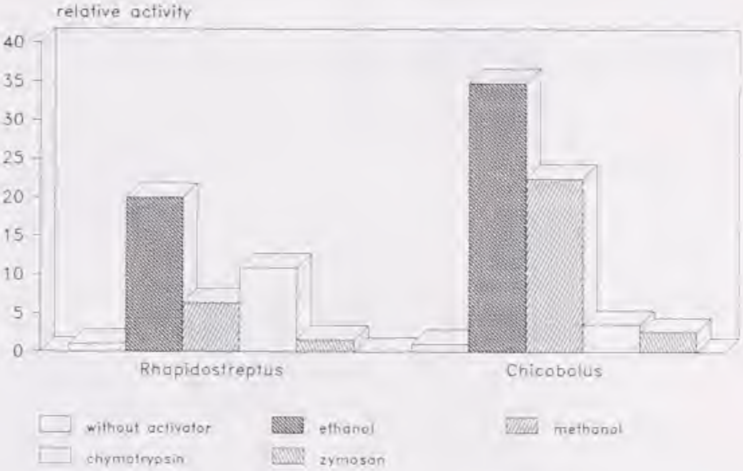


FIG. 3. — Relative in-vitro-activity of the hemolymph of *Rhapidostreptus virgator* and *Chicobolus* sp. without and with application of various potential activators. (activity without activator = 1). Note that the relative activity increase in *Chicobolus* is higher than in *Rhapidostreptus* although the latter has a higher absolute activity.

The activity after chymotrypsin activation increases with elongation of incubation time in both species (Fig. 4); the highest activity is reached after 60 min of incubation. After activation with ethanol the molecular weight (MW) of the PO-active band in SDS-PAGE does not differ from unactivated hemolymph whereas after activation with α-chymotrypsin two different bands occur with lower MW (XYLANDER & BOGUSCH, 1992), indicating that during ethanol activation - in contrast to α-chymotrypsin - a conformational change of the proPO leads to its activity rather than a protein cleavage.

Source : MNHN, Paris

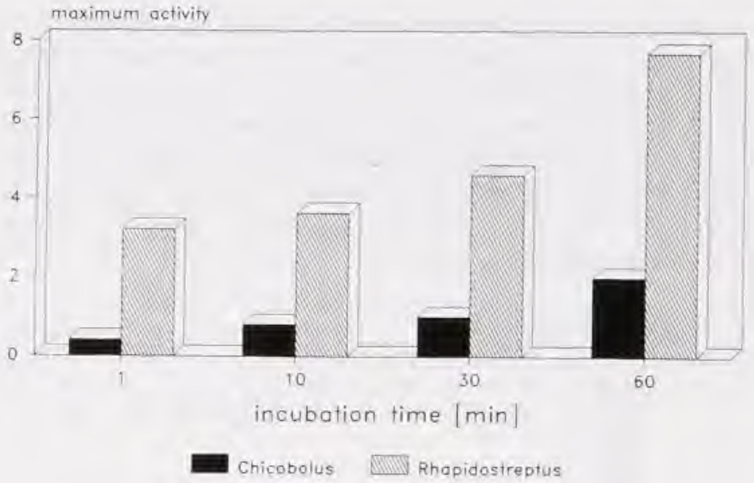


FIG. 4. — PO activity after preincubation of hemolymph samples [min^{-1} ml $hemolymph^{-1}$], from *Rhapidostreptus virgator* and *Chicobolus* sp. with bovine α-chymotrypsin for 1, 10, 30 and 60. The activity of the PO increases in both species with duration of chymotrypsin incubation.

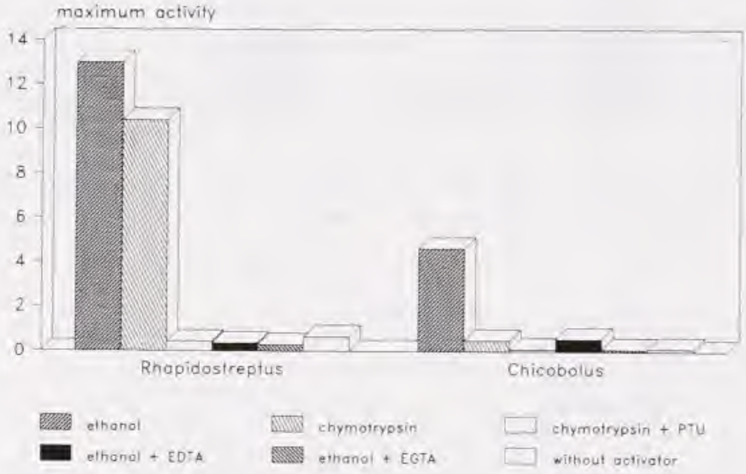


FIG. 5. — Activity of ethanol and of α-chymotrypsin activated and unactivated hemolymph samples [min^{-1} ml $hemolymph^{-1}$] from *Rhapidostreptus* and *Chicobolus* with or without potential PO-inhibitors.

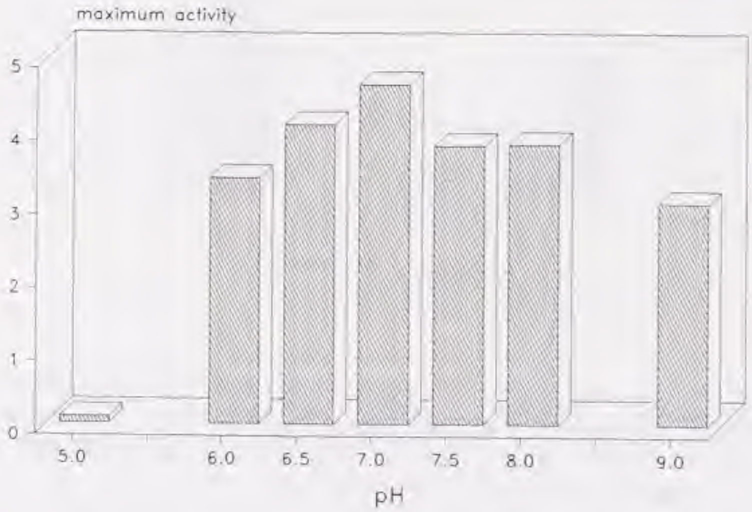
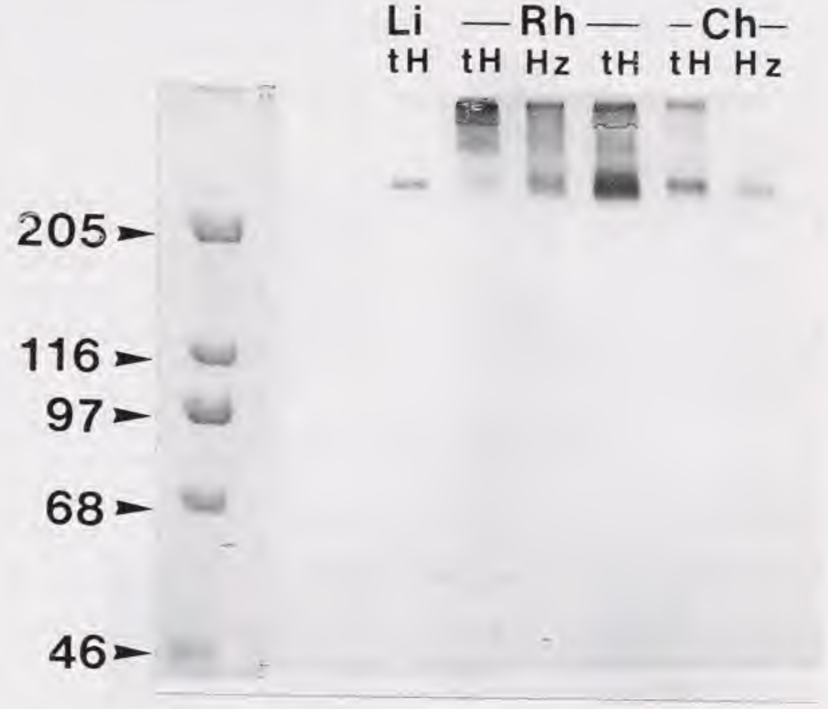


FIG. 6. — Activity of PO [min^{-1} ml $hemolymph^{-1}$] from the hemolymph of *Chicobolus* at different pH.

Source : MNHN, Paris

FIG. 7. — Polyacrylamid-gel (7.5% acrylamid) of hemolymph (tH) and hemocyte lysate (Hz) of *Lithobius forficatus* (Li), *Rhapidostreptus* (Rh) and *Chicobolus* (Ch), with subsequent reactivation of enzymes by incubation in a 2% Triton-X 100 aqueous solution for 30 min, washing in buffer and incubation in an 0.02 M dopa solution in 0.01 M cacodylate buffer (pH 7.0). At the position of reactivated PO dopachrom and melanin is formed resulting in pinkish and later brownish or black band. Molecular standard (SDS-6H, Sigma, Munich) run in the same gel indicates the MW of the PO (corresponding at about 230 kD in all three species).



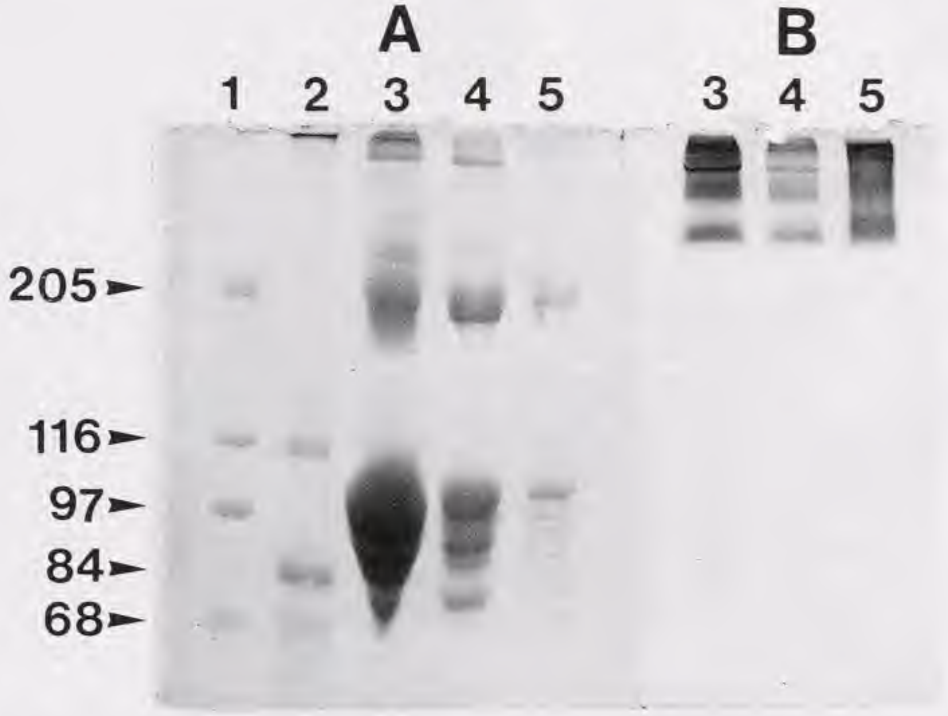


FIG. 8. — PAGE of hemocyte lysate, total hemolymph and plasma of *Rhapidostreptus* (run under the same conditions and with subsequent procedure described for Fig. 7). The left part of the gel was stained with Coomassie Brillant Blue, the right treated as described for Fig. 7). No difference in MW is visible.

Source : MNHN, Paris

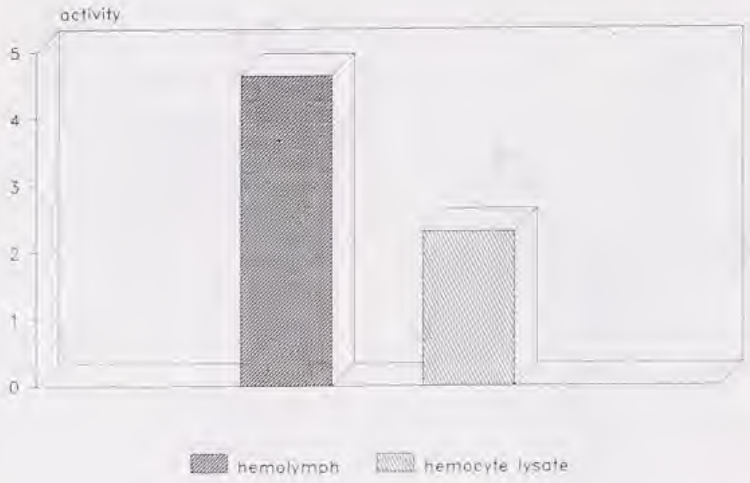


FIG. 9. — PO-activity of *Chicobolus* in the hemocyte lysate (obtained after moderate centrifugation at about 60-100 g at 4°C for 10 min) and hemolymph after ethanol activation.

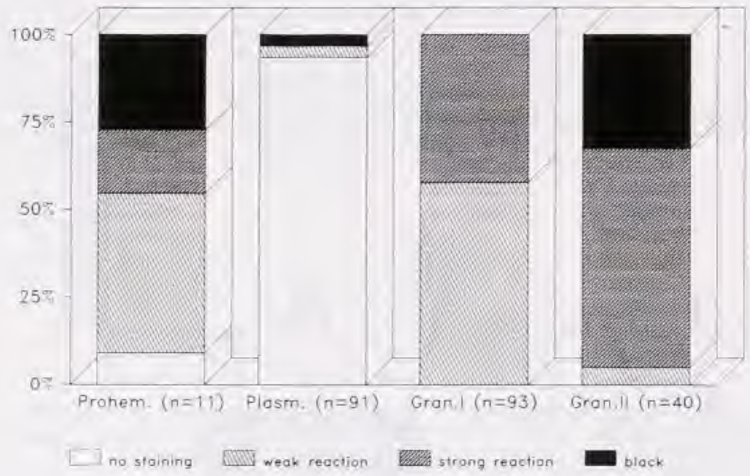


FIG. 10. — Staining capabilities of hemocyte monolayers (in % of each hemocyte type) on glass slides of *Chicobolus* after ethanol activation and dopa incubation.

Microbial activators (zymosan, murein, bacterial lipopolysaccharides) which are potent inductors of PO-reaction in other arthropods have little effect neither on total hemolymph nor on hemocyte lysate (Figs 2 & 3 and unpubl. results); therefore, another activation mechanism may occur in Diplopoda than in Decapoda and Insecta.

Dopa is the substrate used best by the PO of EtOH-activated hemolymph from *Rhapidostreptus* and *Chicobolus* as dopamin and pyrrogallol are less effectively used and tyrosin, pyrocatechol and norephedrin hardly at all (see also XYLANDER & BOGUSCH, 1992).

The PO can be inhibited in the two diplopods and *Lithobius* by phenylthiourea and at least in the diplopods by EDTA and EGTA (Fig. 5) indicating that the PO is of the tyrosinase-type and Ca^{2+} dependend. The pH-optimum of the PO in both diplopods is pH 7.0, although the activity is rather high between pH 6.0 and 8.0 (Fig. 6; see also XYLANDER & BOGUSCH, 1992 for results on *Rhapidostreptus*).

SDS-PAGE under non-reducing conditions

After SDS-PAGE under non-reducing conditions, reactivation of enzymes by incubation in Triton-X 100 and incubation in dopa brownish to black bands occur at the position in the gel of the PO and proPO, respectively. The proPO has corresponding molecular weights (MW) of

Source : MNHN, Paris

about 230 kD in *Lithobius*, *Rhapidostreptus* and *Chicobolus* (Fig. 7). After incubation with α-chymotrypsin the MW is reduced to about 200 and 180 kD whereas EtOH has no such effect (XYLANDER & BOGUSCH, 1992). PO-active bands have the same MW in hemocyte lysate, total hemolymph and plasma of *Rhapidostreptus* (Fig. 8).

Localization of the proPO

After moderate centrifugation of hemolymph of *Rhapidostreptus virgator* at 4°C at about 60-100 g, resuspension and sonification of the hemocyte pellet the activity was mainly (about 80%) found in the hemocyte lysate whereas only little (about 20%) occurred in the plasma (XYLANDER & BOGUSCH, in prep.); hemolymph samples from the same pool not centrifuged had about the sum of plasma and hemocyte lysate activity. Investigations with *Chicobolus* with the same procedure led to degranulation of hemocytes and artificially high activity in the plasma (Fig. 9); if hemolymph was poured into the same amounts of ice-cold hemocyte stabilizing buffer (after SÖDERHÄLL *et al.*, 1979) about half of the activity occured in the hemocytes.

Investigations of glutaraldehyd-fixed hemocyte monolayers of *Rhapidostreptus* and *Chicobolus* after activation with ethanol and subsequent dopa-overlay showed that PO-activity occured mainly in the granular hemocytes (with different intensities which could be designed to two types of granular hemocytes with different spreading capabilities; FIG. 10). Plasmatocytes remained unstained whereas the prohemocytes showed high variability in their PO-reaction (Figs 10 & 11). PTU in control hemocyte monolayers inhibits intracellular PO reaction in both species.

Exocytosis of the PO system in *Rhapidostreptus* cannot be initiated by addition of solutions of various microbial cell wall components as it has been found in insects and crustaceans (JOHANSSON & SÖDERHÄLL, 1985, 1989a, b, c).

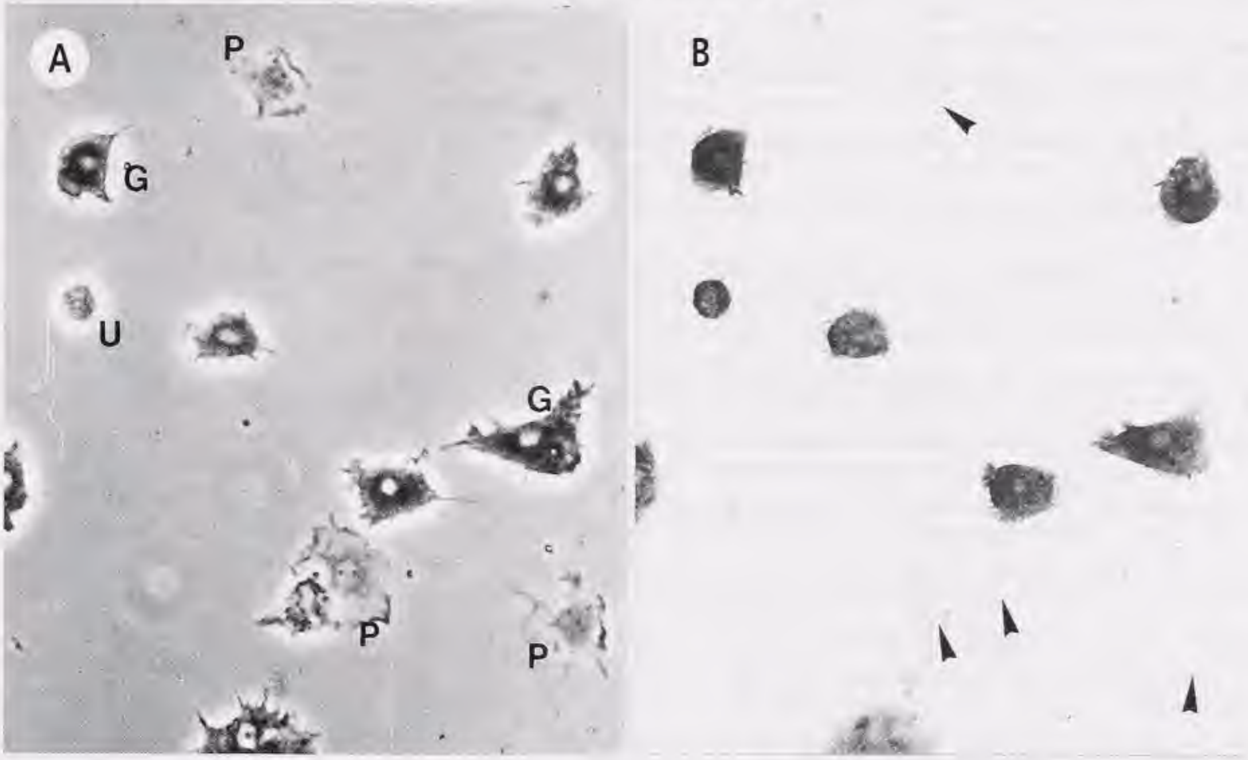


FIG. 11. — Granular hemocytes and plasmatocytes of *Chicobolus* in a hemocyte monolayer. A. Phase contrast. B. Bright field. Only the stained granular hemocytes are visible under these conditions. P: plasmatocytes; G: Granular hemocyte; U: Prohemocyte.

Source : MNHN, Paris

DISCUSSION AND CONCLUSION

As in other arthropods the PO of diplopods occurs in the hemolymph as inactive proPO. Activators found to be efficient in the diplopods also have been reported to activate the proPO of insects and crustaceans (cf. ASHIDA & YAMAZAKI, 1990; GÖTZ, 1988; JOHANSSON & SÖDERHÄLL, 1989b). However, microbial cell wall components (murein, ß-1,3-glucans, lipopolysaccharides from outer cell membrane of Gram-negative bacteria) which activate the proPO in insects and crustaceans (ASHIDA *et al.*, 1983; ASHIDA & SÖDERHÄLL, 1984; ASHIDA & YOSHIDA, 1988; JOHANSSON & SÖDERHÄLL, 1989b; SMITH & SÖDERHÄLL, 1983; SÖDERHÄLL, & HÄLL, 1984; SÖDERHÄLL & UNESTAM, 1979; SÖDERHÄLL *et al.*, 1988) and have been considered to be the inducers of in vivo PO-reactions did not have any effect on diplopods with the system used (XYLANDER, 1992; XYLANDER & BOGUSCH, 1992, this paper). Regarding other capabilities (PTU-inhibition, pH-optimum, Ca^{2+} dependence, preference for dopa as substrate) the proPO and PO of diplopods correspond to that of insects, crustaceans and the few chilopods investigated.

The MW of the two diplopods and *Lithobius* ranges at about 230 kD. This is higher than most data found in most insects and crustaceans the PO and proPO of which have a MW of 60-80 kD; however, corresponding MW (higher than 200 kD) have also been reported for various crustaceans and insects (NELLAIAPPAN *et al.*, 1989; YAMAURA *et al.*, 1980). ASPAN & SÖDERHÄLL (1991) and GILLESPIE *et al.* (1991) reported that the proPO tends to aggregate to form polymeres indicating that the bands found could be a distinctive polymere (tetramere?) of the proPO (cf. ASPAN & SÖDERHÄLL, 1991). Own investigations using gel filtration chromatography of hemolymph of *Rhapidostreptus* (data not shown), however, also led to MW of more than 230 kD of the proPO.

Whether the proPO of arthropods occurs mainly free in the hemolymph or in the hemocytes depends on the taxon investigated. In most insects and all crustaceans investigated, the proPO is predominantly located in the hemocytes; it is discharged and activated after infections (cf. JOHANSSON & SÖDERHÄLL, 1989b; ASHIDA & YAMAZAKI, 1990). In some insects, however, the proPO is reported to occur free in the plasma (GÖTZ *et al.*, 1987, SAUL *et al.*, 1987). In *Rhapidostreptus* the majority of the proPO is also found intracellularly (XYLANDER & BOGUSCH, in prep.), whereas in *Chicobolus* (probably as a preparation artifact due to unsufficient stabilization of hemocytes in a crayfish saline) only about 50% are found in the hemocyte lysate.

In all diplopods and chilopods investigated the granular hemocytes are the site of proPO localization (BOWEN, 1968; KRISHNAN & RAVINDRANATH, 1973; NEVERMANN *et al.*, 1991; XYLANDER & NEVERMANN, 1993), whereas only few plasmatocytes show a faint staining after dopa incubation; the spherulocytes of chilopods are PO-negative (NEVERMANN *et al.*, 1991; XYLANDER & NEVERMANN, 1993). In chilopods staining is rather slow in comparison to diplopods (XYLANDER & NEVERMANN, 1993).

Although microbial cell wall components do not initiate exocytosis of the PO cascade as in crustaceans and insects (cf. reviews in JOHANSSON & SÖDERHÄLL, 1989b; ASHIDA & YAMAZAKI, 1990) rather strong melanization can be found at wound margins of diplopods. This indicates that the PO is activated after an injury or infection and is involved in subsequent immune response: one function of this enzyme may be to support rapid wound closure and to kill bacteria and fungi before they enter the hemocoel and may lead to dangerous infections. Furthermore, an intracellular activation has been found in hemocytic aggregates around foreign material in vitro and in vivo (NEVERMANN, 1989; NEVERMANN & XYLANDER, this volume). As in other arthropods where intracellular activation has been reported (VOLKMANN, 1991; NAYAR *et al.*, 1992) the "melanized hemocytes" in the capsule may constitute an efficient barriere for metabolic waste from potential parasites and invaders on one hand and for nutrients from the hemolymph necessary for their survival on the other hand. Thus melanized hemocytes

Source : MNHN, Paris

may support the function of a multilayered hemocyte capsule formed around parasites as a typical cellular defence reaction of arthropods.

ACKNOWLEDGEMENTS.

I would like to thank O. BOGUSCH, H. -U. JAHN, L. NEVERMANN, A. HUDEL, and Prof. Dr. P. GÖTZ for their support. Investigations and participation in the CIM congress were supported by the President of the Justus-Liebig-University Giessen.

REFERENCES

ASHIDA, M., ISHIZAKI Y. & IWAHANA H., 1983. — Activation of pro-phenoloxidase by bacterial cell walls or ß-1,3 glucans in plasma of the silkworm, *Bombyx mori*. *Biochem. Biophys. Res. Comm.* **113** : 562-568.

ASHIDA, M. & SÖDERHAÄLL, K., 1984. — The prophenoloxidase activating system in crayfish. *Comp. Biochem. Physiol.*, **77B** : 21-26.

ASHIDA, M. & YAMAZAKI H. I., 1990. — Biochemistry of the phenoloxidase system in insects: with special reference to its activation. *In* : E. OHNISHI & H. ISHIZAKI, *Molting and metamorphosis*. Tokyo, Japan Sci. Soc. Press, Berlin, Springer-Verlag : 239-265.

ASHIDA, M. & YOSHIDA H., 1988. — Limited proteolysis of prophenoloxidase during activation by microbial products in insect plasma and effect of phenoloxidase on electrophoretic mobilities of plasma proteins. *Insect Biochem.*, **18** : 11-19.

ASPAN, A. & SÖDERHÄLL, K., 1991. — Purification of prophenoloxidase from crayfish blood cells, and its activation by an endogenous serine proteinase. *Insect Biochem.*, **21** : 363-373.

BOWEN, R. C., 1968. — Tyrosinase in millipede hemocytes. *Trans. Amer. Microsc. Soc.*, **87** : 390-392.

CHADWICK, J. M. & ASTON, W. P., 1978. — An overview of insect immunity. *In* : GERSHWIN, M. E. & E. L. COOPER. *Animal models of comparative and developmental aspects of immunity and diseases*. Oxford, Pergamon Press : 1-14.

GILLESPIE, J. P., BIDOCHKA, M. J. & KHACHATOURIANS, G. G., 1991. — Separation and characterization of grasshopper hemolymph phenoloxidases by sodium dodecyl sulfate-polyacrylamide gel electrophoresis. *Comp. Biochem. Physiol.*, **98C** : 351-358.

GÖTZ, P., 1988. — Immunreaktionen bei Wirbellosen, insbesondere Insekten. *Verh. Dtsch. Zool. Ges.*, **81** : 113-129.

GÖTZ, P., ENDERLEIN, G. & ROETTGEN, I., 1987. — Immune reactions of *Chironomus* larvae (Insecta: Diptera) against bacteria. *J. Insect Physiol.*, **33** : 993-1004.

GÖTZ, P. & VEY, A., 1974. — Humoral encapsulation in Diptera (Insecta) - defense reactions of *Chironomus* larvae against fungi. *Parasitology*, **68** : 193-205.

JOHANSSON, M. W. & SÖDERHÄLL, K., 1985. — Exocytosis of the prophenoloxidase activating system from crayfish haemocytes. *J. Comp. Physiol.*, **B156** : 175-181.

JOHANSSON, M. W. & SÖDERHÄLL, K., 1989a. — A peptide containing the cell adhesion sequence RGD can mediate degranulation and cell adhesion of crayfish granular haemocytes in vitro. *Insect Biochem.*, **19** : 573-579.

JOHANSSON, M. W. & SÖDERHÄLL, K., 1989b. — Cellular immunity in crustaceans and the proPO system. *Parasitology Today*, **5** : 171-176.

JOHANSSON, M. W. & SÖDERHÄLL, K., 1989c. — A cell adhesion factor from crayfish haemocytes has degranulating activity towards crayfish granular cells. *Insect Biochem.*, **19** : 183-190.

KRISHNAN, G. & RAVINDRANATH, M. H., 1973. — Phenoloxidase in the blood cells of millipedes. *J. Insect Physiol.*, **19** : 647-653.

NAYAR, J. K., MIKARTS, L. L., KNIGHT, J. W. & BRADLEY, T. J., 1992. — Characterization of the intracellular melanization response in *Anopheles quadrimaculatus* against subperiodic *Brugia malayi* larvae. *J. Parasitol.*, **78** : 876-880.

NELLAIAPPAN, K., VINAYAGAM, A. & KALYANI, R., 1989. — Electrophoretic pattern of blood and cuticular phenoloxidase of different crustaceans. *Exp. Biol.*, **48** : 177-179.

NEVERMANN, L., 1989. — Licht- und elektronenmikroskopische Untersuchungen der Haemocyten von *Lithobius forficatus* und ihre Bedeutung für zelluläre Abwehrreaktionen. Diploma-thesis, University of Giessen, 69 pp.

NEVERMANN, L., XYLANDER, W. E. R. & SEIFERT, G., 1991. — The hemocytes of the centipede *Lithobius forficatus* (Chilopoda, Lithobiomorpha) - Light and electron microscopic studies using in-vitro techniques. *Zoomorphology*, **110** : 317-327.

PYE, A. E., 1974. — Microbial activation of prophenoloxidase from immune insect larvae. *Nature*, **251** : 610-613.

RATCLIFFE, N. A., LEONARD, C. & ROWLEY, A. F., 1984. — Prophenoloxidase activation: Nonself recognition and cell cooperation in insect immunity. *Science*, **226** : 557-559.

Source : MNHN, Paris

SAUL, S. J., BIN, L. & SUGUMARAN, M., 1987. — The majority of prophenoloxidase in the hemolymph of *Manduca sexta* is present in the plasma and not in the hemocytes. *Dev. Comp. Immunol.*, **11** : 479-485.

SMITH, V. & SÖDERHÄLL, K., 1983. — ß-1,3 Glucan activation of crustaceans hemocytes in vitro and in vivo. *Biol. Bull.*, **164** : 299-314.

SÖDERHÄLL, K., 1982. — Prophenoloxidase activating system and melanization - a recognition mechanism of arthropods? A review. *Dev. Comp. Immunol.*, **6** : 601-611.

SÖDERHÄLL, K. & HÄLL, L., 1984. — Lipopolysaccharide-induced activation of prophenoloxidase activating system in crayfish haemocyte lysate. *Biochim. Biophys. Acta*, **797** : 99-104.

SÖDERHÄLL, K., HÄLL, L., UNESTAM, T. & NYHLEN, L., 1979. — Attachment of phenoloxidase to fungal cell walls in arthropod immunity. *J. Inv. Pathol.*, **34** : 285-294.

SÖDERHÄLL, K., RÖGENER, W., SÖDERHÄLL, I., NEWTON, R. P. & RATCLIFFE, N. A., 1988. — The properties and purification of a *Blaberus craniifer* plasma protein which enhances the activation of haemocyte prophenoloxidase by a ß-1,3-glucan. *Insect Biochem.*, **18** : 323-330.

SÖDERHÄLL, K. & UNESTAM, T., 1979. — Activation of serum prophenoloxidase in arthropod immunity. The specificity of cell wall glucan activation and activation by purified fungal glycoproteins of crayfish phenoloxidase. *Can. J. Microbiol.*, **25** : 406-414.

VEY, A. & GÖTZ, P., 1975. — Humoral encapsulation in Diptera (Insecta) - comparative studies in vitro. *Parasitology*, **70** : 77-86.

VOLKMANN, A., 1991. — Localization of phenoloxidase in the midgut of *Periplaneta americana* parasitized by larvae of *Moniliformis moniliformis* (Acanthocephala). *Parasitol. Res.*, **77** : 616-621.

XYLANDER, W. E. R., 1992. — Immune defense reactions of Myriapoda - A brief presentation of recent results. [*In* : E. MEYER, K. THALER & W. SCHEDL, *Advances in Myriapodology*.] *Ber. nat.-med. Verein Innsbruck*, **Suppl. 10** : 101-110.

XYLANDER, W. E. R. & BOGUSCH, O., 1992. — Investigations on the phenoloxidase of *Rhapidostreptus virgator* (Arthropoda, Diplopoda). *Zool. Jb. Physiol.*, **96** : 309-321.

XYLANDER, W. E. R. & BOGUSCH, O., (in prep.) — The Prophenoloxidase of the millipede *Rhapidostreptus virgator* (Diplopoda, Spirostreptidae) is mainly located in the granular hemocytes.

XYLANDER, W. E. R. & NEVERMANN, L., 1990. — Antibacterial activity in the hemolymph of Myriapoda (Arthropoda). *J. Inv. Pathol.*, **56** : 206-214.

XYLANDER, W. E. R. & NEVERMANN, L., 1993. — Phenoloxidase-active hemocytes in *Lithobius forficatus*, *Scolopendra cingulata* (Chilopoda) and *Chicobolus* sp. (Diplopoda). *Verh. Dtsch. Zool. Ges.*, **86** : 197.

YAMAURA, I., YONEKURA, M., KATSURA, Y., ISHIGURO, M. & FUNATUSU, M., 1980. — Purification and some physico-chemical properties of phenoloxidase from the larvae of housefly. *Agric. Biol. Chem.*, **44** : 55.

Source : MNHN, Paris

In vitro Cellular Immune Reactions of Hemocytes against Bacteria and their Differential Degradation in Myriapods

Lutz NEVERMANN & *Willi E. R.* XYLANDER

Institut für Allgemeine und Spezielle Zoologie, Justus-Liebig-Universität Giessen
Stephanstr. 24, D-35390 Giessen, Germany

ABSTRACT

In vitro the hemocytes of various diplopods and chilopods are capable of phagocytosis and degradation of bacteria. The sequence of this process depends on the myriapod species and the type of bacteria. In *Rhapidostreptus virgator* many *Micrococcus luteus* have been phagocytosed but occur uneffected after 4 hours whereas *E. coli* shows indications of lysis. After 20 hours *M. luteus* also has been degradated. In *Lithobius forficatus*, nodules, aggregations of hemocytes phagocytosing bacteria, are formed when hemocytes are added to a bacterial culture which is turned around continuously. During this process, the hemocytes degranulate. *M. luteus* is lysed within 1 hour when phagocytosed or even located close to a hemocyte cell. *Enterobacter cloacae* is enclosed extracellulary within the matrix of the nodule and subsequently phagocytosed. *E. coli* was not aggregated within the nodule but hemocytes discharged vesicular content onto their surface. They become phagocytosed but do not show indications of lysis after 1 hour. In *Scolopendra cingulata* hemocytes also form nodules with bacteria in the continuously moved culture. These nodules contain a large extracellular matrix in which the bacteria are embedded. Only very few bacteria are phagocytosed within 1h of incubation and there are no signs of lysis in *M. luteus*.

RÉSUMÉ

Réactions immunitaires in vitro d'hémocytes contre des bactéries et leur dégradation chez les myriapodes (Diplopoda & Chilopoda).

In vitro, les hémocytes de différents diplopodes et chilopodes sont capables de phagocyter et de dégrader des bactéries. La séquence de ces processus dépend des espèces de myriapodes et de bactéries. Au bout de 4 heures, chez *Rhapidostreptus virgator*, de nombreux *Micrococcus luteus* sont phagocytés mais ne subissent aucun dommage, tandis que *E. coli* montre déjà des indices de lyse. Au bout de 20 heures, *M. luteus* est, lui aussi, dégradé. Chez *Lithobius forficatus*, de petits nodules se forment, agrégations d'hémocytes phagocytant des bactéries, si des hémocytes sont ajoutés à une culture bactérienne continuellement remuée. Durant ce processus, les hémocytes dégranulent. *M. luteus* est lysé en 1 heure, si les bactéries sont phagocytées ou même seulement se trouvent à proximité d'un hémocyte. *Enterobacter cloacae* se trouve inclus de manière extracellulaire dans la matrice du nodule, puis phagocyté. *E. coli* ne montre pas d'agrégation en nodules, mais les hémocytes déchargent le contenu de certaines vésicules sur la surface bactérienne. Elles seront finalement phagocytées mais aucune trace de lyse n'est visible au bout de 1 heure. Chez *Scolopendra cingulata*, les hémocytes forment des nodules avec les bactéries en culture. Ces nodules contiennent une volumineuse matrice extracellulaire dans laquelle les bactéries sont incorporées. Au bout de 1 heure, seul un très petit nombre d'entre elles est phagocyté ou lysé.

NEVERMANN, L. & XYLANDER, W. E. R., 1996. — In vitro cellular immune reactions of hemocytes against bacteria and their differential degradation in myriapods. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 421-430. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

INTRODUCTION

Two mechanisms are involved in defense of arthropods against infections by microorganisms: the formation of antibacterial substances which in insects mainly act free in the plasma, and the action of defense cells e. g. hemocytes which form nodules or phagocytose the microbes. Lysozyme, an enzyme depolymerizing the cell wall of Gram-positive bacteria, is permanently found in the hemolymph (DUNN, 1986; GÖTZ, 1988) whereas most antibacterial substances against Gram-positive bacteria are formed within a few hours after an external stimulus, e. g. infections or injury (cf. BOMAN, 1986; GÖTZ, 1988). Therefore, nodule formation and phagocytosis are the initial defense mechanisms against microbes that help to absorb infective bacteria until other mechanisms are available.

The mechanisms and the procedure of cellular defense against bacteria has been well documented in insects, whereas little is known about such processes in "myriapods". This paper, therefore, describes nodule formation, phagocytosis, specificity of phagocytic hemocytes to different bacteria and degradation of ingested bacteria in the diplopod *Rhapidostreptus virgator* and the chilopods *Lithobius forficatus* and *Scolopendra cingulata*.

MATERIAL AND METHODS

Animals

Specimens of *Scolopendra cingulata* were collected in 1990 at different sites in northern Spain and maintained solitary since then in large bellaplast boxes with 2 cm of clean sand or soil covered with paper towels at room temperature at a shaded place. Humidity of the substratum was controlled weekly and moistened with tab water if necessary. Specimens were fed with *Acheta domesticus*, *Tenebrio molitor* mainly larvae and *Sarcophaga* sp. mainly imagines. *Lithobius* and *Rhapidostreptus* were obtained and reared as described by XYLANDER & NEVERMANN (1990). Hemolymph was obtained as specified earlier (XYLANDER & NEVERMANN, 1990; XYLANDER & BOGUSCH, 1992) and dropped directly into the culture medium.

Hemocyte preparations

For investigations with hemocytes of *Rhapidostreptus* hemolymph was added to a 1 cm^2 piece of gelatine foil after swelling it in I-Ringer (11 g NaCl, 7 g KCl, 5.5 g $CaCl_2$, in 1l H_2O) for 30 min in culture dishes. Hemocytes were allowed to adhere to the substratum in I-Ringer for 50 min at room temperature. Then 10 µl of a bacterial suspension were added. Hemocytes cultures with bacteria were slowly moved on a shaker for 1 h, 4 h and 20 h.

For investigations on chilopods 10 µl of suspended "washed" bacteria (see below) were added to 1 ml LAH (*Lithobius*-artificial-hemolymph according to WENNING,1989) in an Eppendorf cap and then 10 µl freshly collected hemolymph was supplied. The Eppendorf caps were fixed with cello tape to a spinbar and rotated vertically on a magnetic stirrer for 1 h at room temperature. Subsequently, the Eppendorf cap was centrifuged at 100 x g for about a minute, the supernatant was removed and the pellet was processed for electron microscopy.

Preparation of bacterial cultures

The bacteria used in this study were obtained from Prof. Dr. P. GÖTZ, Berlin (*Micrococcus luteus*, *Enterobacter cloacae* ß-12 and *Escherichia coli* K12 D31). Bacteria were cultivated in nutrient broth (Merck Standard I) over night at 35°C in a water bath. Small amounts of this "over-night-culture" were added to fresh broth and raised until optical density reached 0.65 at 565 nm.

For investigations on chilopods 1 ml of bacteria in culture were washed twice by centrifugation (room temperature, 5 min at 1000 x g) and resuspension of the bacterial pellet to 1 ml with LAH. Finally, 10 µl of the resuspension were added to the hemocyte culture.

Preparation for transmission electron microscopy

All samples were fixed in 2.5% glutaraldehyde, 2% paraformaldehyde in 0.1 M sodium cacodylate buffer, pH 7.0 for 2 h at 4-6°C, washed in buffer, postfixed in 2% OsO_4, dehydrated through an acetone series and embedded in araldite. Semithin and ultrathin sections were made on a Reichert OmU3 ultracut microtome, mounted on formvar coated copper grids, stained with uranyl acetate and lead citrate and investigated with a Zeiss EM 9 A transmission electron microscope (TEM).

RESULTS

Rhapidostreptus

Within 4 h after addition of bacteria the hemocytes of *Rhapidostreptus* have phagocytosed both Gram-negative *E. coli* and Gram-positive *Micrococcus luteus* (Figs 1, 2, 5 & 6). The bacteria are located in vacuoles mainly in that part of the hemocytes without contact to the

Source : MNHN, Paris

substratum (Figs 1 & 5); the vacuoles have been found to be smaller around *Micrococcus* than around *E. coli* (Figs 1 & 5). Most *Micrococcus* remain rather uneffected and still show their typical electron dense internal structure (Figs 1 & 2) whereas the inside of *E. coli* occurs less electron dense and flocculent indicating degradation (Figs 5 & 6). After 20 h dramatic changes are found. The cell wall of phagocytosed *Micrococcus* has been completely degradated and the bacteria have been killed as noticed from an obvious decrease in their electron density (Figs 3 & 4). Plasmatocytes of *Rhapidostreptus* have disintegrated after 20 h leaving a translucent vesicular cell debris whereas granulocytes look relatively unchanged. Bacteria which have not been phagocytosed still exhibit their normal structure but show electron dense amorphous material at their surface.

Lithobius forficatus

After 1 h in the "stirrer culture" plasmatocytes, granulocytes and some spherulocytes (for description and classification of hemocytes, see NEVERMANN *et al.*, 1991) have aggregated to form nodules (Fig. 7). Plasmatocytes and granulocytes, however, no longer can be differentiated, since they have lost most of their grana obviously by exocytosis into the culture medium. All three species of bacteria are phagocytosed. Phagocytic vesicles enclosing bacteria have been observed to fuse with lysosomes and become electron dense (Figs 8, 9, 11 & 16).

Micrococcus is lysed in electron translucent phagocytic vesicles (Fig. 14). Their cell wall is thinned off and their plasm becomes more electron translucent in TEM compared to living bacteria (Figs 14 & 15). Even bacteria attached to the surface of hemocytes or lying in short distance to hemocytes frequently undergo lysis. Bacteria, located in some distance are uneffected (Fig. 15).

Enterobacter, in contrast to *Micrococcus* and *E. coli*, becomes aggregated in the hemolymph culture and, therefore, clusters of bacteria are surrounded by hemocytes (Fig. 7). Nevertheless, some of the bacteria are phagocytosed and lysed (Figs 7-9). In one single phagocytic vesicle different stages of bacterial lysis may be found. Destroyed bacteria swell and occur less electron dense (Figs 7 & 8).

E. coli are not aggregated but show a scattered distribution throughout the hemocyte nodule. They become phagocytosed occasionally but no indications of lysis was found after 1 h of culture neither in translucent nor in electron dense phagocytic vesicles (Figs 10-13). Prior to phagocytosis fibrous material from the so-called structured vesicles (see NEVERMANN *et al.*, 1991) is discharged onto the surface of *E. coli* (Fig. 10). The same material may also be found in phagocytic vesicles containing bacteria (Fig. 12).

Scolopendra cingulata

The hemocytes of *S. cingulata* aggregate to form nodules which contain an voluminous, possibly fibrous, extracellular material (Fig. 17). Many bacteria (only *Micrococcus* was tested) are embedded in this matrix and most of them seem to have no contact to the hemocytes. Nevertheless, some bacteria are phagocytosed. As in *Lithobius* the phagocytic vesicles of *Scolopendra* may have an electron dense matrix but - in contrast to *Lithobius* - *Micrococcus* does not get lysed (Fig. 16). Presumably, in this species it takes more time than 1 h until visible signs of lysis are found in TEM.

DISCUSSION

Phagocytosis has been described for insects in a number of papers but for other groups of arthropods there is only very little information on phagocytosis and intracellular degradation of microbes by hemocytes (e. g. JOHNSON, 1981; PALM, 1953; TYSON & JENKIN, 1973). The TEM-micrographs of phagocytosis in arthropods, however, are very similar indicating that the

Source : MNHN, Paris

mechanisms must be quite alike. Even intracellular degradation of bacteria and the appearance of electron-dense phagocytic vesicles are much alike in insects (cf. ROWLEY & RATCLIFFE, 1976a and our investigation on chilopods).

Two initial mechanisms are involved in host cellular defense reaction against invading bacteria: phagocytosis and nodule formation. Phagocytosis is supposed to be the main reaction against low numbers of bacteria in arthropods (GÖTZ, 1982; CHRISTENSEN & NAPPI, 1988). But when there are high numbers of microbes entering the hemocoel nodule formation occurs (RATCLIFFE & GAGEN, 1977). Our in vitro observations of *Lithobius* and *Scolopendra* indicate that nodule formation and phagocytosis are related processes in the coagulum.

In the spiny lobster, *Panulirus japonicus* a factor is released from granular hemocytes after stimulation with bacteria which provokes clotting of the other hemocyte types (AONO *et al.*, 1993). This implies that even a small number of microbes can elicit clotting. Nodule formation may, therefore, not be restricted to reactions against higher numbers of bacteria but is a general process occurring parallel to phagocytosis.

Lithobius hemocytes can degradate bacteria faster (in only 1 h) than *Scolopendra* and *Rhapidostreptus* and other arthropods investigated. In an *in vitro* investigation with hemocytes of *Calliphora erythrocephala* ROWLEY & RATCLIFFE (1976a) found cell wall damage and swollen bacteria not before 2 h of incubation. Heat killed bacteria *Bacillus cereus* injected into the hemocoel were entrapped into nodules but they did not show any signs of breakdown even after 24 h (RATCLIFFE & GAGEN, 1977).

The reaction of hemocyte types to different bacteria varies. Granular cells of *Galleria mellonella* make contact with *E. coli* in vitro, get stressed and degranulate (ROWLEY & RATCLIFFE, 1976b). Eventually, they may phagocytose *E. coli* but most bacteria remain attached to the outside of the cells. The plasmatocytes of this species remain unstressed and phagocytose bacteria and the decaying granular cells. However, no killed bacteria have been observed. In this investigation all hemocyte types were involved in phagocytosis and nodule formation. In *Rhapidostreptus* granular hemocytes even seemed to be more stable and less sensible to lysis than plasmatocytes.

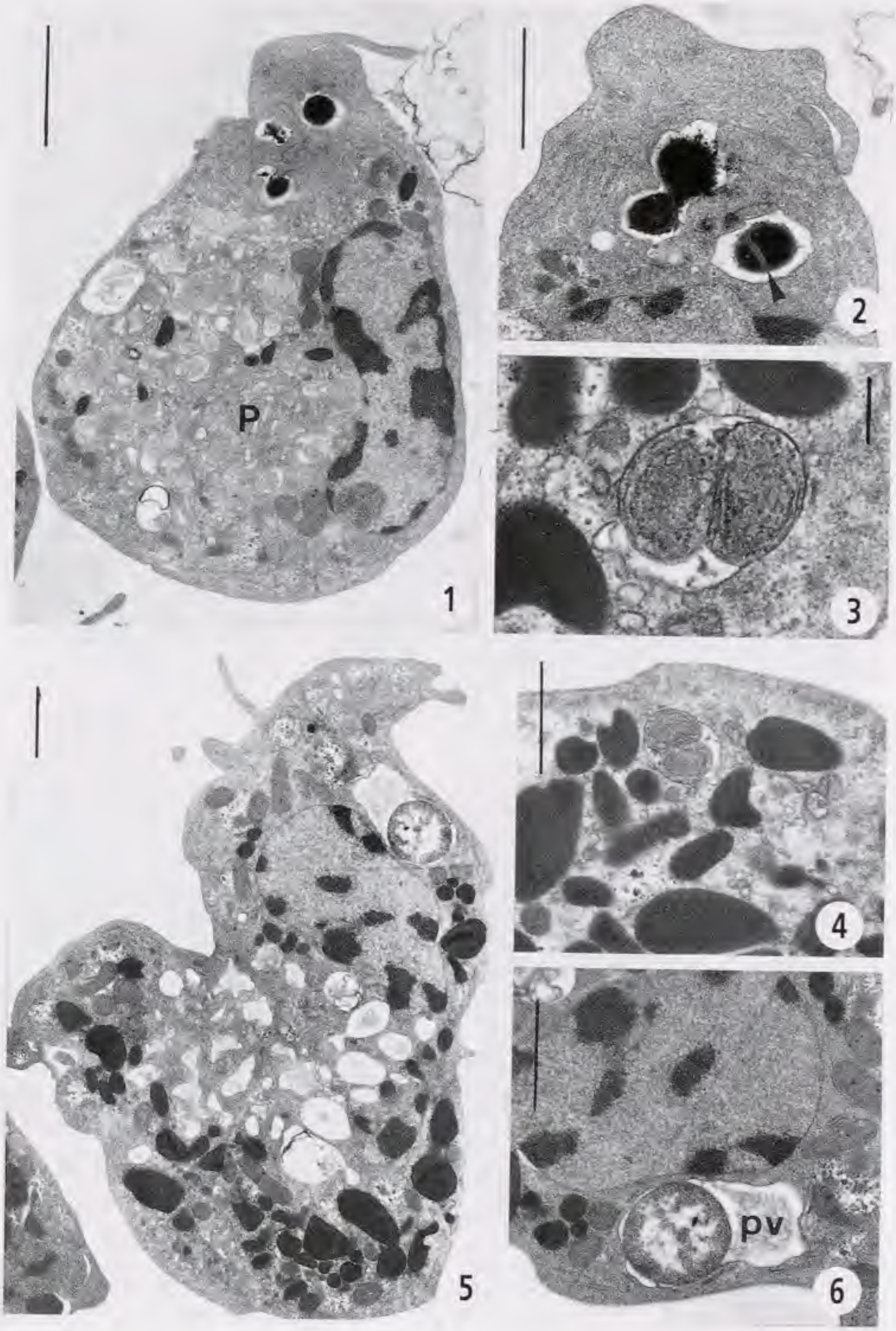
FIGS 1-6. — *Rhapidostreptus virgator*: 1. Plasmatocyte (P) containing some not lysed *Micrococcus luteus* in phagocytic vesicles, 4 h of incubation. Scale bar: 2 µm. 2. Plasmatocyte with phagocytosed *M. luteus*, 4 h of incubation. The diplococcal structure of the bacteria is visible (arrowhead). Scale bar: 1 µm. 3. Granulocyte (II) with phagocytosed *M. luteus* which has become translucent due to lysis, 20 h of incubation. Scale bar: 0.2 µm. 4. Granulocyte (II) with phagocytosed lysed *M. luteus*, 20 h of incubation. Scale bar: 1 µm. 5. Granulocyte (I) with phagocytosed and lysed *E. coli*, 4 h of incubation. The phagocytic vesicle surrounding the bacterium is significantly larger than that around *M. luteus*. Scale bar: 1 µm. 6. Granulocyte (I) with lysed *E. coli* in the phagocytic vesicle (pv) showing a flocculent less electron dense content, 4 h of incubation. Scale bar: 1 µm.

FIGS 7-9. — *Lithobius forficatus*: 7. Hemocytic nodule. Plasmatocytes (P) forming a primary capsule around agglutinated *Enterobacter cloacae* (E). Arrowheads indicate bacteria just being phagocytosed. Scale bar: 5 µm. 8. Large electron dense phagocytic vesicle (pv) containing *E. cloacae* in various stages of degradation. Scale bar: 1 µm. 9. Fusion of an electron dense lysosome with a phagocytic vesicle containing *E. cloacae*. Scale bar: 0.5 µm.

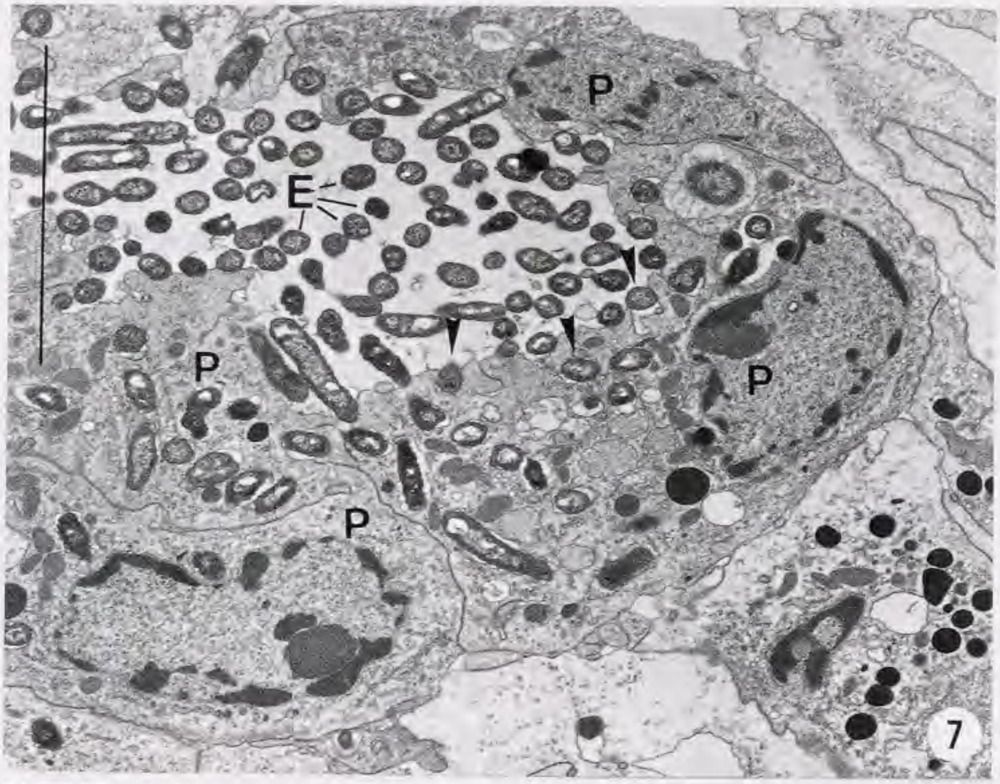
FIGS 10-13. — *Lithobius forficatus*: 10. *E. coli* during phagocytosis. Note fibrous material (*) discharged onto bacteria. 11. Electron dense phagocytic vesicle (pv) with five *E. coli* without clear indications of lysis. 12. Phagocytic vesicle of a granular hemocyte with structured content (sv) and phagocytosed *E. coli*. The cell shows signs of disintegration. 13. Small translucent vesicles (arrow) gathering around phagocytosed *E. coli*. All scale bars on this plate: 1 µm.

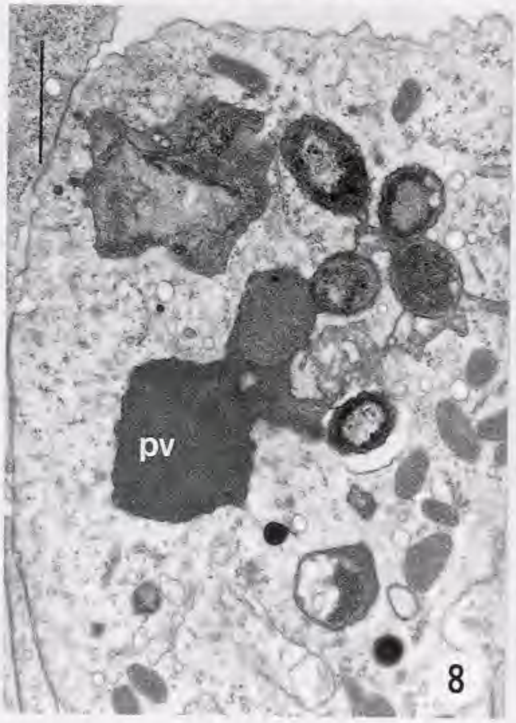
FIGS 14-15. — *Lithobius forficatus* & FIGS 16-17.— *Scolopendra cingulata*: 14. Phagocytosed and lysed *Micrococcus luteus* (M). Note the thinned murein sacculus. The hemocytes have lost most of their grana. Scale bar: 5 µm. 15. Few still electron dense *M. luteus* with an intact murein sacculus (arrow) at some distance to a hemocyte. Bacteria located closer are more electron translucent on lysis. Arrowhead: semi-lysed diplococcus. Scale bar: 1 µm. 16. Four *M. luteus* in an electron dense phagocytic vesicle (pv) without signs of degradation. Scale bar: 1 µm. 17. Nodules of *S. cingulata* with an voluminous extracellular matrix (X) embedding the hemocytes and *M. luteus* (M). Some bacteria are being phagocytosed (Mp). Scale bar: 1 µm.

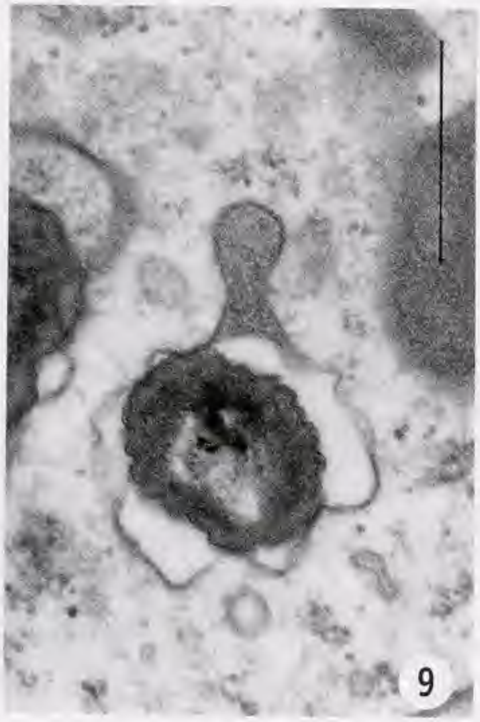
Source : MNHN, Paris



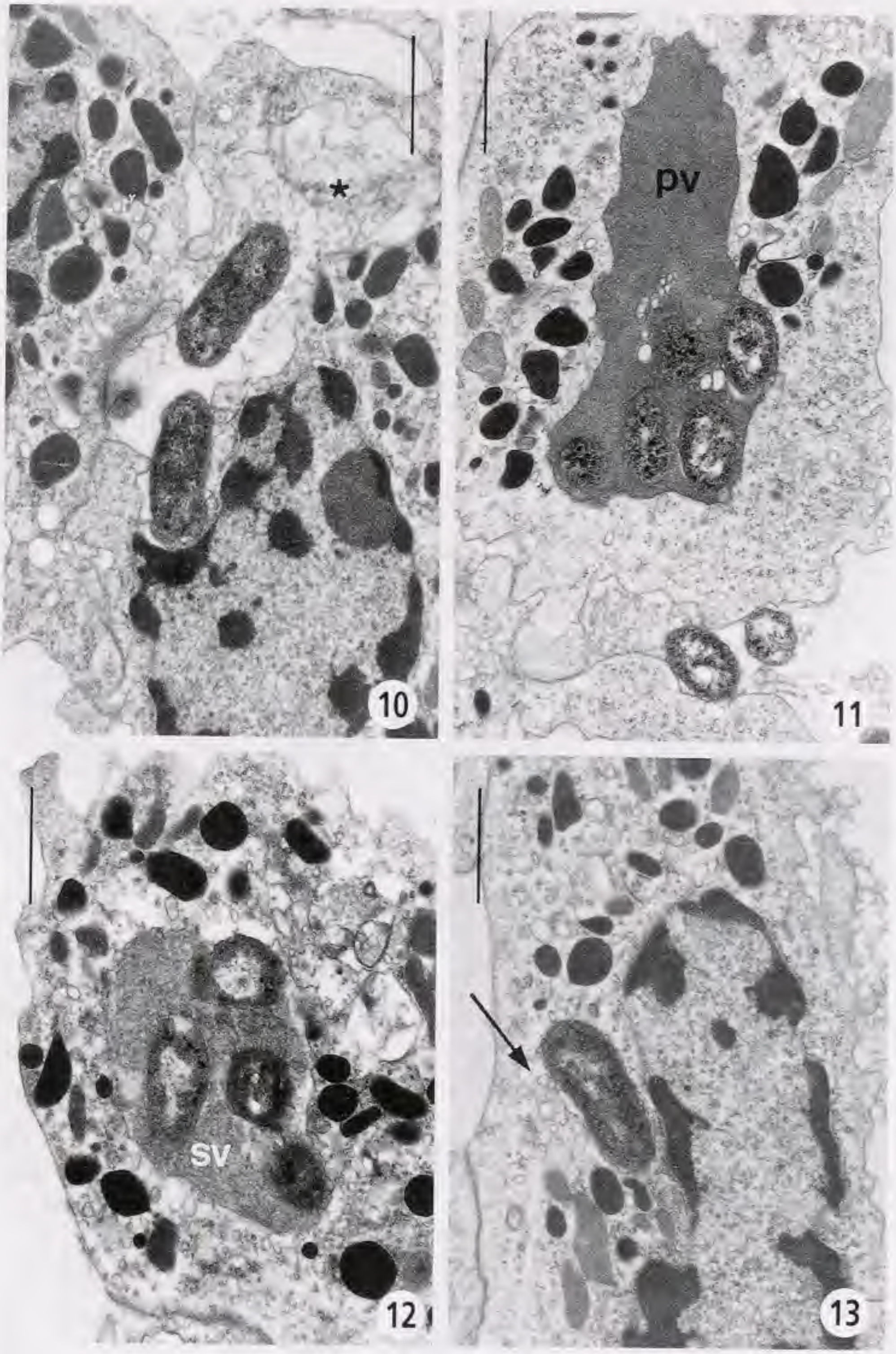
Source : MNHN, Paris



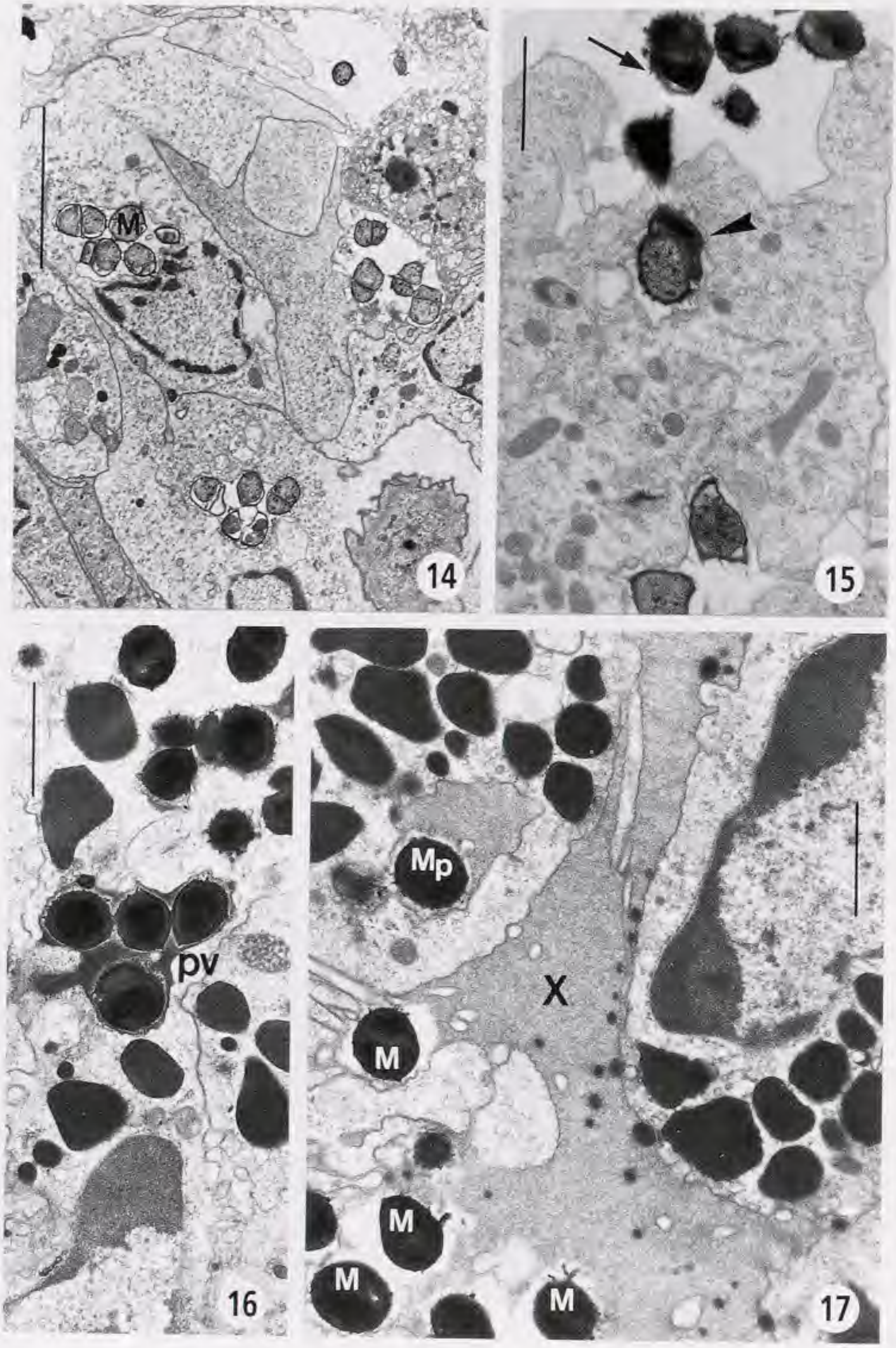




Source : MNHN, Paris



Source : MNHN, Paris



Source : MNHN, Paris

The time span until bacterial degradation becomes visible differs in the species investigated and may be due to antibacterial substances which have earlier been demonstrated by bacterial-agar diffusion tests in various diplopods and chilopods (VAN DER WALT *et al.*, 1990; XYLANDER & NEVERMANN, 1990). Antibacterial substances produced by hemocytes may be involved in the intracellular and extracellular degradation of bacteria as observed. The thinning of the cell wall of *Micrococcus luteus* indicates the action of lysozym which also has been shown to occur in the hemolymph of various diplopods and chilopods (XYLANDER & NEVERMANN, 1990). In the investigations by XYLANDER & NEVERMANN (1990), *Scolopendra oraniensis* and *Rhapidostreptus* had less effect on living bacteria than e. g. *Lithobius*; especially the lysozyme effect on lyophilized *Micrococcus luteus* was low. Thus, the delay in cell wall lysis in *Scolopendra* and *Rhapidostreptus* may be caused by lower titers of lysozym available in the hemocytes. This corresponds to recent immunocytochemical detection of varying amounts of lysozyme in hemocytes of chilopods (NEVERMANN, unpublished).

In many insects investigated the fat body is the main site of synthesis of antibacterial substances after infections; they are discharged into the hemolymph where they destroy bacteria. Hemocytes may also produce such substances (TRENCZEK, 1988) but their importance in insects for humoral antibacterial defense seems to be low. However, in other arthropods like crustaceans (FENOUIL & ROCH, 1991; SMITH & CHRISHOLM, 1992), xiphosurans (MURAKAMI *et al.*, 1991; NAKAMURA *et al.*, 1988; TOH *et al.*, 1991), diplopods (XYLANDER, unpublished) and chilopods (NEVERMANN, unpublished), the antibacterial substances are mainly located in the hemocytes which most probably also are the site of their formation. Located in the hemocytes the antibacterial substances may be strongly involved in killing and subsequent or simultaneous lysis of bacteria. This could probably be the original function (and site of formation) of the antibacterial substances in arthropods; in insects or a subgroup of this taxon the fat body seems to have taken over this function from hemocytes. Thereby, the antibacterial defense may have become subdivided in an initial cellular and a subsequent humoral phase.

However, further proteins may be involved in the cellular defense against bacteria. Agglutination of bacteria as found in *Lithobius* could be due to lectins which have been found in the hemolymph plasma of different diplopods (JAHN & SEIFERT, 1992; JAHN & XYLANDER, 1991; XYLANDER, 1990, 1992) and may - as shown in e. g. insects (PENDLAND *et al.*, 1988) - be responsible for bacterial agglutination and opsonization facilitating phagocytosis.

ACKNOWLEDGEMENTS

We would like to thank Miss A. HUDEL for printing the micrographs and the President of the Justus-Liebig-University, Giessen, who supported this investigation and our participation in the congress.

REFERENCES

AONO, H., OOHARA, I. & MORI, K., 1993. — Cell type-specific roles in the hemocyte clotting system of the spiny lobster, *Panulirus japonicus*. *Comp. Biochem. Physiol.*, **105A** : 11-15.

BOMAN, H. G., 1986. — Antibacterial immune proteins in insects. *In* : A. M. LACKIE, *Immune mechanisms in invertebrate vectors. Symp. Zool. Soc., London* , **56** : 45-58.

CHRISTENSEN, B. M. & NAPPI, A. J., 1988. — Immune responses of arthropods. *ISI Atlas of Science, Animal and Plant Sciences* : 15-19.

DUNN, P. E., 1986. — Biochemical aspects of insect immunology. *Ann. Rev. Entomol.*, **31** : 321-339.

FENOUIL, E. & ROCH, P. 1991. — Evidence and characterization of lysozyme in six species of freshwater crayfishes from Astacidae and Cambaridae families. *Comp. Biochem. Physiol.*, **B 99** : 43-49.

GÖTZ, P., 1982. — Wie Insekten sich gegen Krankheitserreger und Parasiten verteidigen. *Sitzungsber. Ges. Naturforsch. Freunde Berlin N. F.*, **22** : 33-48.

GÖTZ, P., 1988. — Immunreaktionen bei Wirbellosen, insbesondere Insekten. *Verh. Dtsch. Zool. Ges.*, **81** : 113-129.

JAHN, H. U. & SEIFERT, G.,1992. — Humorale Lektine in der Haemolymphe von *Rhapidostreptus virgator*. *Verh. Dtsch. Zool. Ges.*, **85** : 263.

Source : MNHN, Paris

JAHN, H. U. & XYLANDER, W. E. R., 1991. — Lektine bei *Rhapidostreptus* - Bestandteile des Immunsystems? *In* : W. SCHONER & M. KRÖGER, *3. Werkstattberichte aus der Experimentellen Biologie und Experimentellen Medizin*. Giessen, Universität Giessen : 53.

JOHNSON, P. T., 1981. — Histopathology of *Aerococcus viridans var. homari* infection *Gaffkemia* in the lobster, *Homarus americanus*, and a comparison with histological reactions to a gram-negative species, *Pseudomonas perolens*. *J. Inv. Pathol.*, **38** : 127-148.

MURAKAMI, T., NIWA, M., TOKUNAGA, F., MIYATA, T & IWANAGA, S., 1991. — Direct virus inactivation of Tachyplesin I and its isopeptides from horseshoe crab hemocytes. *Chemotherapy*, **37** : 327-334.

NAKAMURA, T., FURUNAKA, H., MIYATA, T., TOKUNAGA, F., MUTA, T., IWANAGA, S., NIWA, M., TAKAO, T & SHIMONISHI, Y.,1988. — Tachyplesin, a class of antimicrobial peptides from the hemocytes of the horseshoe crab *Tachypleus tridentatus*. *J. Biol. Chem.*, **263** : 16709-16713.

NEVERMANN, L., XYLANDER, W. E. R. & SEIFERT, G., 1991. — The hemocytes of the centipede *Lithobius forficatus* Chilopoda, Lithobiomorpha: Light and electron microscopic studies using in-vitro techniques. *Zoomorphology* , **110** : 317-327.

PALM, N. B., 1953. — The elimination of injected vital dyes from the blood in Myriapods. *Arkiv Zool.*, **6** : 219-246.

PENDLAND, J. C., HEATH, M. A. & BOUCIAS, D. G., 1988. — Function of a galactose-binding lectin from *Spodoptera exigua* larval haemolymph: opsonization of blastospores from entomogenous hyphomycetes. *J. Insect Physiol.*, **34** : 533-540.

RATCLIFFE, N. A. & GAGEN, S. J., 1977. — Studies on the in vivo cellular reactions of insects: An ultrastructural analysis of nodule formation in *Galleria mellonella*. *Tissue Cell* , **9** : 73-85.

ROWLEY, A. F. & RATCLIFFE, N. A., 1976a. — An ultrastructural study of the in vitro phagocytosis of *Escherichia coli* by the hemocytes of *Calliphora erythrocephala*. *J. Ultrastr. Res*,. **55** : 193-202.

ROWLEY, A. F. & RATCLIFFE, N. A., 1976b. — The granular cells of *Galleria mellonella* during clotting and phagocytic reactions in vitro. *Tissue Cell* , **8** : 437-446.

SMITH, V. J. & CHRISHOLM, J. R. S., 1992. — Non-cellular immunity in crustaceans. *Fish Shellfish Immunol.*, **2** : 1-31.

TOH, Y., MIZUTANI, A.,TOKUNAGA, F., MUTA, T. & IWANAGA, S., 1991. — Morphology of the granular hemocytes of the Japanese horseshoe crab *Tachypleus tridentatus* and immunocytochemical localization of clotting factors and antimicrobial substances. *Cell Tissue Res.*, **266** : 137-147.

TRENCZEK, T., 1988. — Injury and immunity in insects. Studies with *Hyalophora cecropia* fat body and hemocytes in vivo and in vitro. *In* : F. SEHNAL, A. ZABZA & D. L. DENLINGER, *Endocrinological frontiers in physiological insect ecology*. Wroclaw, Wroclaw Technical University Press : 369-378.

TYSON, C. J. & JENKIN, C. R.,1973. — The importance of opsonic factors in the removal of bacteria from the circulation of the crayfish *Parachaeraps bicarcinus*. *Austral. J. Exp. Biol. Med. Sci.*, **51** : 609-615.

VAN DER WALT, E., MCCLAIN, E., PUREN, A. & SAVAGE, N., 1990. — Phylogeny of arthropod immunity. An inducible humoral response in the Kalahari millipede, *Triaenophorus triodus* Attems. *Naturwiss.* , **77** : 189-190.

WENNING, A., 1989. — Transporteigenschaften der Malpighischen Gefäße von *Lithobius forficatus* (L.), Myriapoda, Chilopoda. *Verh. Dt. Zool. Ges.*, **82** : 215-216.

XYLANDER, W. E. R., 1990. — Immune defense reactions of myriapods - recent results and perspectives. *In* : "*8th International Congress of Myriapodology, Abstracts*" . *Veröffentl. d. Universität Innsbruck*: **177** : 65.

XYLANDER, W. E. R., 1992. — Immune defense reactions of Myriapoda - A brief presentation of recent results. [*In* : THALER, K., E. MEYER & W. SCHEDL, *Advances in Myriapodology* .] *Ber. d. naturw.-med. Verein Innsbruck*, **Suppl. 10** : 101-110.

XYLANDER, W. E. R. & BOGUSCH, O., 1992. — Investigations on the phenoloxidase of *Rhapidostreptus virgator* (Arthropoda, Diplopoda). *Zool. Jb. Physiol.*, **96** : 309-321.

XYLANDER, W. E. R. & NEVERMANN, L., 1990. — Antibacterial activity in the hemolymph of Myriapoda Arthropoda. *J. Inv. Pathol.*, **56** : 206-214.

Source : MNHN, Paris

Evidence for Antibacterial Activity in Haemolymph of Diplopoda: Preliminary Results

Grzegorz KANIA *, *Jan* JAROSZ **, *Mariola* ANDREJKO ** & *Malgorzata* STEFANIAK**

* Department of Biology and Parasitology, Medical Academy, 20-080 Lublin, Poland
** Department of Insect Pathology, Marie Curie-Sklodowska University, 20-033 Lublin, Poland

ABSTRACT

In a screening bioassay, the antibacterial activity in haemolymph from eight species of millipedes (*Megaphyllum projectum kochi, Ommatoiulus sabulosus, Unciger foetidus, Polydesmus complanatus, Glomeris connexa, Strongylosoma pallipes* auct., *Leptoiulus proximus, Oxidus gracilis*) was compared with cell-free antibacterial immunity of *Galleria mellonella* pupae. The only millipedes where lysozyme was not constantly detectable are *M. projectum kochi* and *S. pallipes*. In others, the low constitutive titre of lysozyme was unaffected by injections with *Enterobacter cloacae* ß12 or nutrient broth. In *Galleria*, as for the majority of insects, such previously present antibacterial activity increased markedly after preinjection of the pupae with *E. cloacae* or sterile broth. In pupae of *Galleria*, the antibacterial activity of cecropin-like type is induced by *E. cloacae* as well as by non-living material, the broth. A trace activity against *Escherichia coli* D31 was present in untreated *Unciger*, but this titre did not increase after bacterial inoculation. Haemolymph from *M. projectum kochi, P. complanatus* and *O. gracilis* investigated 2 days after injections of either broth or *E. cloacae* did not show any inducible antibacterial activity. Injections of *E. cloacae* into *Ommatoiulus*, but broth into *Glomeris*, induce a measurable antibacterial activity against *E. coli* D31.

RÉSUMÉ

Mise en évidence d'une activité antibactérienne dans l'hémolymphe de Diplopodes.

Chez huit espèces de diplopodes (*Megaphyllum projectum kochi, Ommatoiulus sabulosus, Unciger foetidus, Polydesmus complanatus, Glomeris connexa, Strongylosoma pallipes* auct., *Leptoiulus proximus, Oxidus gracilis*), l'activité antibactérienne de l'hémolymphe a été comparée à l'immunité antibactérienne des pupes de *Galleria mellonella*. Les seuls diplopodes chez lesquels les lyzozymes ne sont pas constamment décelables sont *M. projectum kochi* et *S. pallipes*. Chez les autres espèces, on ne note aucun effet à la suite d'injections de *Enterobacter cloacae* ß12 ou de milieu de culture nutritif. Chez *Galleria*, comme chez la plupart des insectes, l'activité antibactérienne s'accroît significativement après injection de la pupe par *E. cloacae* ou un milieu stérile. Chez la pupe de *Galleria*, l'activité antibactérienne de type cécropine est induite aussi bien par *E. cloacae* que par un milieu non-vivant. Une trace d'activité anti-*Escherichia coli* D31 est présente chez *Unciger* non traité, mais ce taux ne s'accroît pas après une inoculation bactérienne. L'hémolymphe de *M. projectum kochi, P. complanatus* et *O. gracilis*, étudiés deux jours après injection soit de milieu de culture, soit de *E. cloacae*, ne montre aucune activité antibactérienne décelable. Des injections de *E. cloacae* chez *Ommatoiulus* induisent une activité antibactérienne mesurable à l'encontre de *E. coli* D31 alors que cet effet est produit par le milieu de culture chez *Glomeris*.

KANIA, G., JAROSZ, J., ANDREJKO, M. & STEFANIAK, M., 1996. — Evidence for antibacterial activity in haemolymph of Diplopoda : preliminary results. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 431-435. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

INTRODUCTION

Invertebrates can defend themselves against bacterial infections by both cellular (SALT, 1970) and humoral (CHADWICK, 1975) defence mechanisms. A potent humoral immune system that can be induced by an infection with live non-pathogenic bacteria or injections of abiotic foreign bodies is specially well characterized in pupae of Lepidoptera (BOMAN & HULTMARK, 1987) which respond to the infection with *Enterobacter cloacae* by the synthesis of several classes of immune proteins. Humoral immunity in lepidopterans and other holometabolous insects is due mainly to the antibacterial action of lysozyme (MOHRING & MESSNER, 1968) and a new class of small basic polypeptides, the cecropins (BOMAN & HULTMARK, 1987).

The presence of lysozyme in normal and immunized arthropods has been reported in phylogenetically distant species of invertebrates (GOTZ & TRENCZEK, 1991), including myriapods (XYLANDER & NEVERMANN, 1990). Of inducible bactericidal immune proteins that are de novo synthesized by several orders of Insecta, cecropins produced in *Hyalophora cecropia* and other lepidopterans are the first antibacterial factors well defined biochemically.

In this paper we compared the antibacterial activity in haemolymph from eight species of millipedes with the pupal *Galleria mellonella* immune system, using techniques for antibacterial activity assays developed in the study of cell-free insect immune responses.

MATERIALS AND METHODS

Millipedes

Using a cup plate agar-diffusion assay technique, antibacterial activities of lysozyme and cecropins were detected in native (non-immune) and immune haemolymph of diplopod species: *Megaphyllum projectum kochi* (Verhoeff), *Ommatoiulus sabulosus* (L.), *Unciger foetidus* (C. L. Koch), *Polydesmus complanatus* (L.), *Glomeris connexa* C. L. Koch, *Strongylosoma pallipes* (auct.), *Leptoiulus proximus* (Nemec), *Oxidus gracilis* (C. L. Koch). All the millipedes investigated live within woodland litter and soil as their natural habitat. In laboratory, the specimens caged in glass vessels fed plant litter in varying stages of decomposition. Animals were maintained at 12° C until bleeding for bioassays of antibacterial activities.

Induction of immune response and sampling of haemolymphs

For immunization, the millipedes were injected into the abdominal haemocoel with either live, log phase *Enterobacter cloacae* (0.6 x 104 bacteria per specimen) or sterile nutrient broth (3.0 ml), an abiotic soluble foreign molecule. By the same way, two day old pupae of *Galleria mellonella* (Lepidoptera, Pyralidae) taken out of their cocoons were inoculated with immunizing bacteria or nutrient broth. Fully vigorous, unwounded pupae were served as a control because of available already evidence on antibacterial immune proteins active in insect immunity (JAROSZ, 1993). Millipedes treated with foreign bodies were incubated for 48 hours at 12°C, but pupae of *Galleria* at 26°C. Haemolymph from millipedes were obtained after incision of the intersegmental abdominal cuticle, using a sterile glass micropipette. Only small volumes of blood may be collected from each individual, but trace amounts of haemolymph obtained from most of the diplopod species herein investigated were quite sufficient to assay the antibacterial activities in a thin agar layer with the wells of 0.7 mm in diameter.

Bioassays for antibacterial activities

Lysozyme activity (E C. 3.2.1.17; endo-ß-/1-4/-N-acetylmuramide glycanohydrolase) was determined in an inhibition zone assay around the well, using freeze-dried *Micrococcus luteus* incorporated into an agar medium at a concentration of 1.0 mg/ml, according to MOHRIG & MESSNER (1968). The test for haemolymph lysozyme activity was conducted in 0.066 M Sorensen buffer (pH 6.4) with 1.0% agarose and 70 mg/ml streptomycin sulfate to inhibit bacterial contaminations.

Bactericidal activity of cecropins provoked in pupal haemolymph of *Galleria* was quantified as a diameter of the lysis zone around the well in a thin agar layer inoculated with an overnight culture of *Escherichia coli* (about 0.3 x 105 log phase cells per ml), strain D31 sensitive to cecropin-like activity. Haemolymph samples loaded into 0.7 mm diameter wells cut in the soft (0.7%) agar medium, were incubated at 28°C for 36 hours. Agar medium for assay of cecropin activity (but not for lysozyme) contained a trace of phenylthiourea to prevent melanization due to phenoloxidase activity.

Source : MNHN, Paris

RESULTS

The antibacterial activity in haemolymph of non-immunized and *E. cloacae*-, or broth-injected millipedes was compared with the activity of lysozyme and that of cecropins induced in *Galleria* pupae. Though considerable differences in haemolymph lysozyme activity of different individuals and different diplopod species were noticed, the normally low lysozyme activity was unaffected by *E. cloacae* ß12 or broth. The normally low lysozyme titer present in untreated *O. sabulosus, U. foetidus* and *P. complanatus* did not increased in specimens injected with foreign bodies (Table 1). No differences in haemolymph activity were noted between immunized and non-immunized diplopods. In our screening experiments, haemolymph lysozyme was not present in untreated *M. projectum kochi* and *S. pallipes* but a relatively high innate activity of lysozyme was found in *G. connexa* and *L. proximus.* Injections of foreign materials into body cavity of the millipede *O. gracilis* did not increase the hardly any detectable the constitutive antibacterial activity of haemolymph lysozyme. In contrast, the normally high innate lysozyme titer in *Galleria* pupae becomes elevated after bacterial infections (0.4 x 105 *E cloacae*) so much as after injections of broth.

TABLE 1. — Antibacterial activity of lysozyme in haemolymph of non-immunized millipedes and those immunized with *Enterobacter cloacae* or sterile nutrient broth. Tr; trace activity; lysis zone diameter less than 1.0 mm (diameter of wells; 0.7 mm). "-"; not examined because of difficulty in collecting the haemolymph sample.

Diplopod species	Haemolymph lysozyme activity; lysis zone diameter (mm)		
	Non-immunized	Specimens immunized with:	
		Enterobacter cloacae	Sterile nutrient broth
Megaphyllum projectum kochi	0	0	0
Ommatoiulus sabulosus	1.5	1.5	1.5
Unciger foetidus	1.5	1.8	1.6
Polydesmus complanatus	1.7	1.7	1.8
Glomeris connexa	5.0	5.5	5.0
Strongylosoma pallipes auct.	0	-	-
Leptoiulus proximus	4.0	-	-
Oxidus gracilis	Tr	Tr	Tr
Galleria mellonella	8.0	10.5	10.0

In pupae of *Galleria*, cecropin antibacterial activity could normally be provoked by both living *E. cloacae* and sterile broth. Injections of broth (3.0 ml per animal) into body cavity of *G. connexa* can induce within 2 days a measurable antibacterial activity against *E. coli* D31 (Table 2). A similar but less pronounced antibacterial activity could be generated in *O. sabulosus* treated with *E. cloacae*. Other millipedes injected with *E. cloacae* (or broth) did not develop antibacterial activity against *E. coli*. Trace activity directed against *E. coli* was found in immunized and non-immunized *U. foetidus.* Further investigations are, however, needed to elucidate if the antibacterial activity appeared in immunized *G. connexa* and *O. sabulosus* could tentatively be classified to an inducible activity of cecropin-like type. Antibacterial activity against *E. coli* in the haemolymph of *G. connexa* and *O. sabulosus* might be detected only in some

Source : MNHN, Paris

individuals. These inconsistent results may partly be caused by the difficulty in collecting enough haemolymph from these millipedes. Furthermore, many specimens of millipedes treated with *E. cloacae* died just one day after bacterial injections.

TABLE 2. — Efforts to induce the cecropin-like antibacterial activity in haemolymph of Diplopoda by bacterial infections with *Enterobacter cloacae* or inoculations of the millipedes with sterile nutrient broth. Tr; trace activity, lysis zone diameter of *E. coli* D31 less than 1.0 mm (diameter of the well, 0.7 mm). "- "; not examined.

Diplopod species	Cecropin-like activity; lysis zone diameter of *E. coli* (mm)		
	Non-immunized	Specimens immunized with: *Enterobacter cloacae*	Sterile nutrient broth
Megaphyllum projectum kochi	0	0	0
Ommatoiulus sabulosus	0	1.7	Tr
Unciger foetidus	Tr	Tr	Tr
Polydesmus complanatus	0	0	0
Glomeris connexa	0	Tr	4.5
Strongylosoma pallipes auct.	0	-	-
Leptoiulus proximus	0	-	-
Oxidus gracilis	0	0	0
Galleria mellonella	0	8.5	8.0

DISCUSSION

Despite of the progress in insect immunology, only scant evidence are still available about antibacterial substances, both innate and inducible, conditioning humoral immunity in myriapods. Intensive research activity of the last few years has led to the identification of new and interesting groups of peptides with antibacterial activity. It seems that their occurrence is not restricted to insects. XYLANDER & NEVERMANN (1990) have described at least two antibacterial substances in haemolymph of Diplopoda; one substance is lysozyme but the other one is different from lysozyme. Activity against living *Micrococcus luteus* increased after inoculation with *E. cloacae* ß12 in two diplopod species, *Rhapidostreptus virgator* and *Chicobolus* sp. Independently of the bacterial strain used as an immunizing agent, growth of *E. cloacae*, but not *E. coli*, was inhibited by haemolymph (XYLANDER & NEVERMANN, 1990). Thus far, the activity against *E. coli* was detected only in haemolymph from the millipede *Triaenostrepus triodus* (VAN DER WALT *et al.*, 1990), and in haemolymph of immunized diplopods *Ommatoiulus sabulosus* and *Glomeris connexa* (Table 2).

CONCLUSION

The low innate haemolymph lysozyme titer that increases drastically in insects invaded with non-pathogenic bacteria (MOHRIG & MESSNER, 1968) and inducible antibacterial immune proteins like cecropins that are synthesized in the fat body of several insect species (BOMAN & HULTMARK, 1987), but rather absent in millipedes, could confirm the suggestions of RAVINDRANATH (1973) and NEVERMANN & XYLANDER (1992), concerning the crucial role of cellular immune responses in antibacterial defences of Diplopoda. The phenoloxidase system, that is considered to be one of the main systems of immune defense in arthropods being responsible for foreign recognition, killing of microbial invaders, encapsulation of parasites and

Source : MNHN, Paris

wound healing helps the haemocytic reactions in diplopods since the melanization is found at wound margins, in the haemocytic wound closure and in haemocytic capsules around foreign bodies (XYLANDER & BOGUSCH, 1992).

REFERENCES

BOMAN, H. G. & HULTMARK, D., 1987. — Cell-free immunity in insects. *Ann. Rev. Microbiol.*, **41** : 103-126.

CHADWICK, J. S., 1975. — Hemolymph changes with infection or induced immunity in insects and ticks. *In* : K. MARAMOROSH & R. E. SHOPE, *Invertebrate Immunity*, New York, Academic Press : 241-271.

GÖTZ, P. & TRENCZEK, T., 1991. — Antibacterial proteins in insects other than Lepidoptera and Diptera and in some other invertebrates. *In* : A. P. GUPTA, *Immunology of Insects and other Arthropods* . London, CRC Press, Boca Raton : 323-346.

JAROSZ, J., 1993. — Induction kinetics of immune antibacterial proteins in pupae of *Galleria mellonella* and *Pieris brassicae*. *Comp. Biochem. Physiol.*, **106B** : 415-421.

MOHRIG, W. & MESSNER, B., 1968. — Immunoreaktionen bei Insekten. I. Lysozym als grundlegender antibakterieller Factor im humoralen Abwehrmechanismus der Insekten. *Biol. Zentralbl.*, **87** : 439-470.

NEVERMANN, L. & XYLANDER, W. E. R., 1992. — Cellular immune responses in centipedes and millipedes (Arthropoda, Tracheata). *In* : *XXV Annual Meeting of Society for Invertebrate Pathology, Heidelberg, Aug. 16 - 21*, Germany : 124.

RAVINDRANATH, M. H., 1973. — The hemocytes of a millipede, *Thyropygus poseidon*. *J. Morphol.*, **141** : 257-268.

SALT, G., 1970. — *The Cellular Defense Reactions of Insects*. Cambridge, Cambridge University Press.

VAN DER WALT, A., MCCLAIN, A. E., PUREN, A. & SAVEGE, N., 1990. — Phylogeny of arthropod immunity. An inducible humoral response in the Kalahari millipede, *Triaenostreptus triodus* (Attems). *Naturwiss.*, **77** : 189-190.

XYLANDER, W. E. R. & NEVERMANN, L., 1990. — Antibacterial activity in the hemolymph of Myriapoda (Arthropoda). *J. Invertebr. Pathol.*, **56** : 206-214.

XYLANDER, W. E. R. & BOGUSCH, O., 1992. — Investigations on the phenoloxidase of *Rhapidostreptus virgator* (Arthropoda, Diplopoda). *Zool. Jb. Physiol.*, **96** : 309-321.

Source : MNHN, Paris

Source : MNHN, Paris

Supernumerary Malpighian Tubules in Chilopods

Carol Constantin PRUNESCU *& Paula* PRUNESCU

Institute of Biology, 296 Spl. Independentei, RO-79651 Bucharest, Romania

ABSTRACT

In Chilopoda, up to now, one pair of Malpighian tubules was described. These tubules are inserted on each side of the gut at the junction of the mid and the hind-gut. In *Scutigera coleoptrata* an additional pair of Malpighian tubules is present, differing from the main one by its smaller diameter and in being dorsally and ventrally inserted on the gut, at the same level as the main pair, through small vesicles. In *Craterostigmus tasmanianus*, in addition to the main Malpighian tubules, there is a third one, inserted dorsally, in the median plane, and orientated backwards. Animals belonging to Lithobiidae, Henicopidae and Geophilomorpha show only the main pair. Additional Malpighian tubules of *Scutigera* and *Craterostigmus* may represent plesiomorphic characters.

RÉSUMÉ

Tubules de Malpighi surnuméraires chez les chilopodes.

Jusqu'à présent, on a décrit chez les chilopodes une seule paire de tubules de Malpighi. Les tubules sont insérés (un sur la partie gauche, l'autre sur la partie droite de l'intestin) au niveau de la jonction de l'intestin moyen (glandulaire) avec l'intestin postérieur. Chez *Scutigera coleoptrata* les deux tubules supplémentaires de Malpighi, avec un diamètre plus petit, sont insérés sur la partie dorsale et ventrale de l'intestin au même niveau que la paire principale. Chez *Craterostigmus tasmanianus*, un tubule de Malpighi supplémentaire, un troisième, est inséré dorsalement, dans le plan médian et orienté vers l'extrémité postérieure du corps. Les recherches réalisées chez les Lithobiidae, Henicopidae et Geophilomorpha ont démontré la présence d'une seule paire de tubules de Malpighi. La présence de tubules de Malpighi surnuméraires chez *Scutigera* et *Craterostigmus* peut être considérée comme un caractère plésiomorphe.

INTRODUCTION

All previous data concerning the anatomy of the Malpighian tubules indicates the existence of only one pair of Malpighian tubules in chilopods (LEWIS, 1981). A study of the microscopic anatomy permits the description of some supplementary Malpighian tubules in *Scutigera coleoptrata* and *Craterostigmus tasmanianus*.

MATERIAL AND METHOD

Specimens of *S. coleoptrata* (males, females and larvae) were collected in Sicily (Italy) in 1969 and in Dobrogea (Romania) between 1967 and 1992. Fixation was made in Bouin's solution or 70% ethylic alcohol. A material constituted by the caudal part of the body of two females of *C. tasmanianus*, embedded in paraffin, was offered to us by S. M. MANTON in 1964. This material was from Tasmania. Also from Tasmania were some females and males of *C. tasmanianus* gathered by R. MESIBOV in 1991. This material was fixed in formaldehyde-calcium (S. M. MANTON's lot) or in glutaraldehyde 2.5% in cacodylat buffer (R. MESIBOV's lot). The material was processed according normal histological technique.

PRUNESCU, C. C. & PRUNESCU, P., 1996. — Supernumerary malpighian tubules in chilopods. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 437-440. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

RESULTS

In *Scutigera coleoptrata*, transverse serial sections, taken through the junction of the mid-gut and hind-gut, confirmed the opening of the two main Malpighian tubules in the horizontal (bilateral) plane (Figs 1-2). Before the opening, each of the Malpighian tubules present an ampulla which narrows at the level of the opening in the intestine. Approximately at the same level, two other Malpighian tubules open into the intestine, but in a dorso-ventral plane. One of these Malpighian tubules opens in the median-dorsal plane and the other in the median-ventral plane (Figs 3-5). Before opening into the intestine, each of the dorso-ventral Malpighian tubule presents its own, small ampulla. The dorso-ventral Malpighian tubules are extended and coiled along the mid-gut, like the main pair of Malpighian tubules. We cannot make any statement about the length of the dorso-ventral Malpighian tubules.

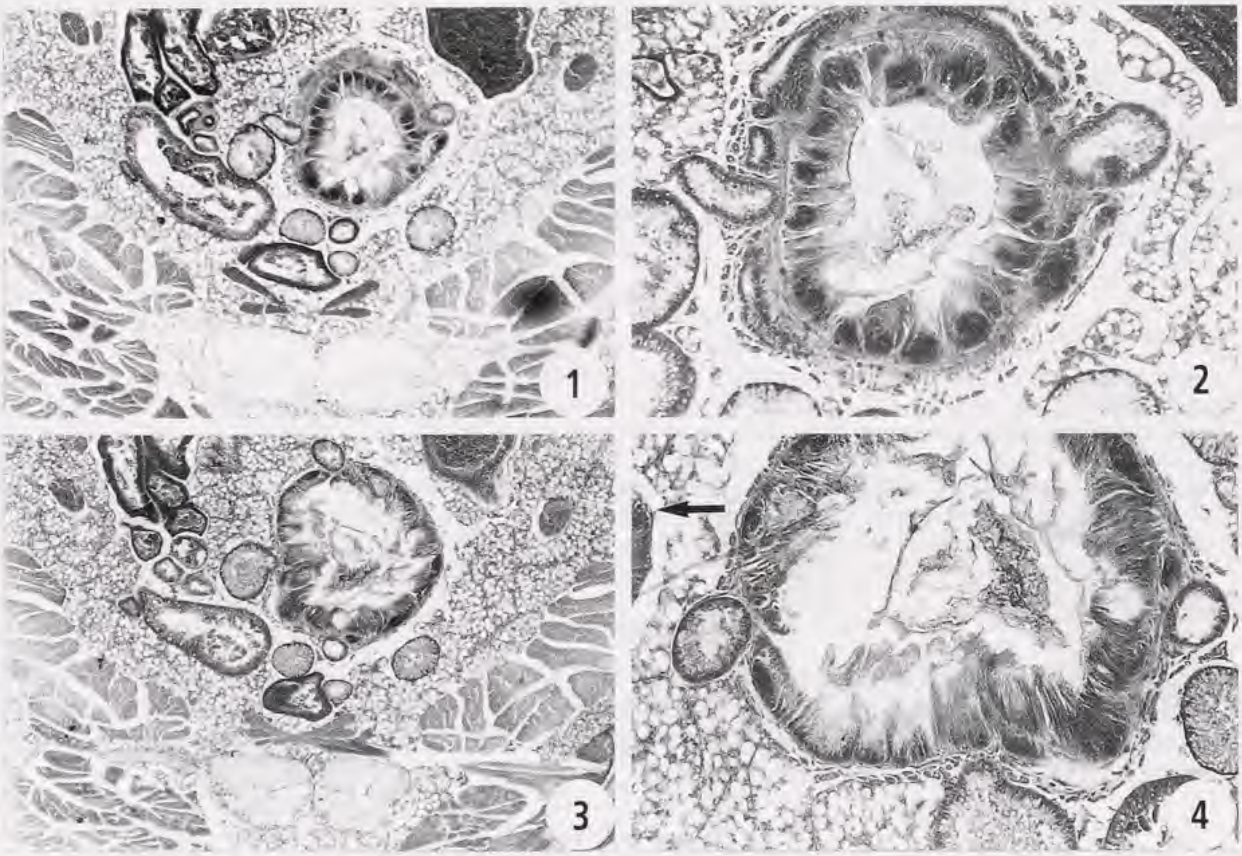


FIG. 1. — Lateral Malpighian tubules opening into the intestine (*S. coleoptrata*), H-e. x80.
FIG. 2. — Detail of the opening of the lateral Malpighian tubules at the level of the junction of the mid and hind-gut (*S. coleoptrata*) x160.
FIG. 3. — Opening of the dorso-ventral Malpighian tubules into the gut (*S. coleoptrata*) x80.
FIG. 4. — Detail of FIG. 3. x200. The arrow shows the top of the slide.

FIG. 6. — Dorsal Malpighian tubule (arrow) (*C. tasmanianus*) x400. (see next page FIG. 6-9).
FIG. 7. — Dorsal Malpighian tubule drawn near the dorsal wall of the gut (arrow). — The lateral Malpighian tubules ampullas open into the intestine (*C. tasmanianus*). x120.
FIG. 8. — Dorsal Malpighian tubule opening into the dorso-median zone of the intestine (arrow) (*C. tasmanianus*) x120.
FIG. 9. — Detail of the opening of the dorsal Malpighian tubule (arrow). (*C. tasmanianus*) x400. →

Source : MNHN, Paris

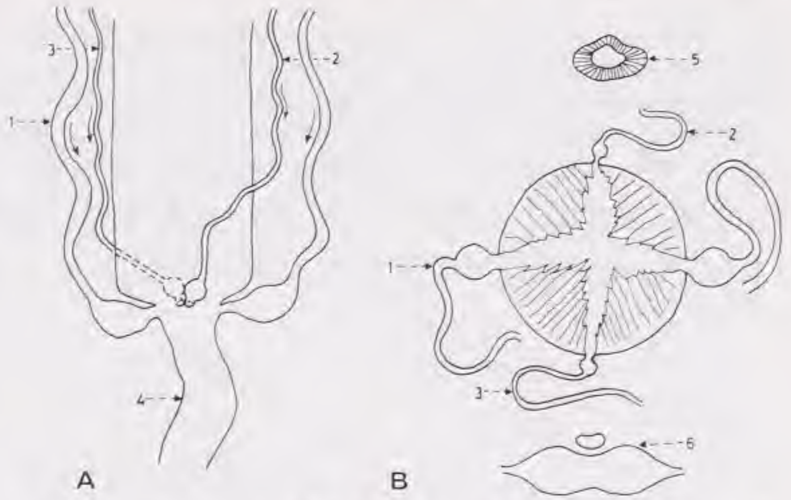
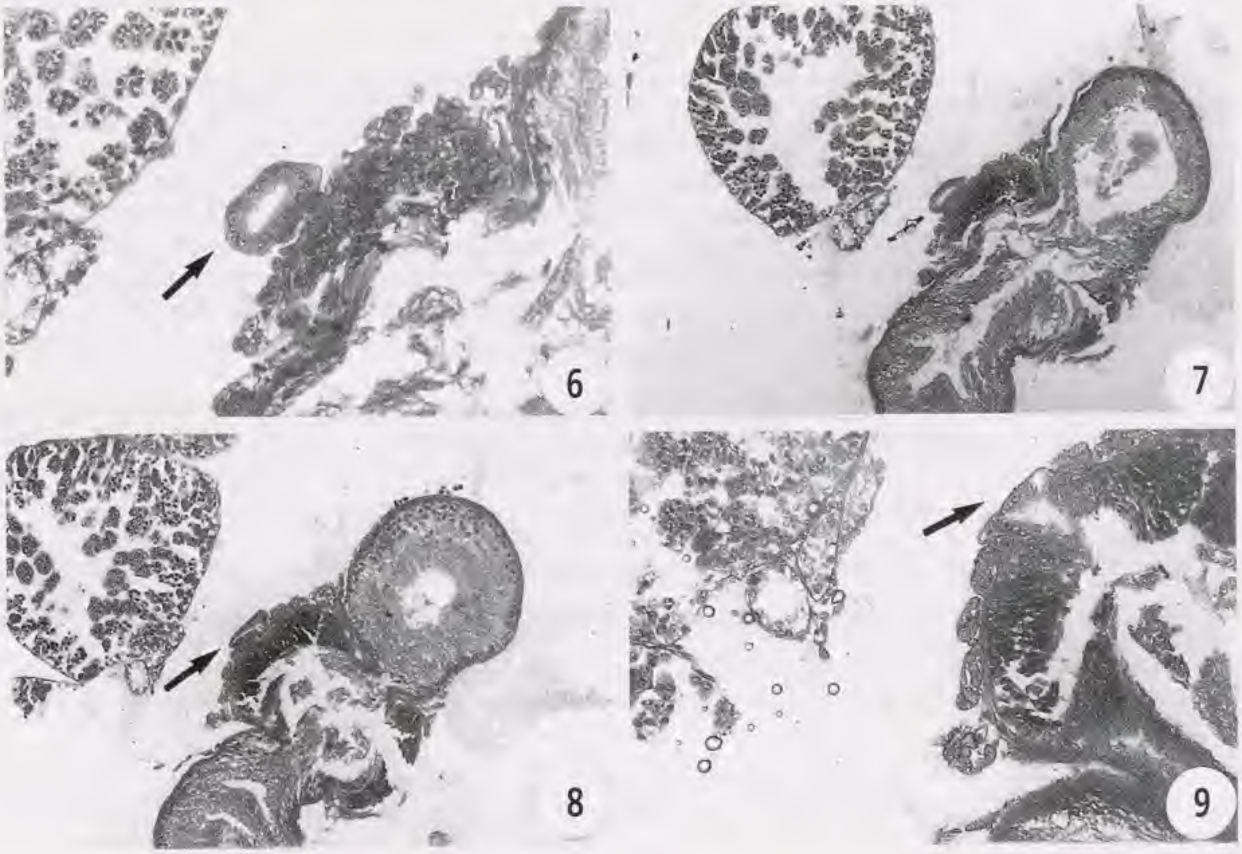


FIG. 5. — Schematic representation of the insertion of the Malpighian tubules of *Scutigera coleoptrata*.
A: dorsal view;
B: Transversal section;
1: lateral Malpighian tubule;
2: dorsal Malpighian tubule;
3: ventral Malpighian tubule;
4: hind-gut;
5: vas dorsalis;
6: ventral nerve ganglia.

In *Craterostigmus tasmanianus*, the laterally-inserted Malpighian tubules show an ampulla of great size at their proximal end (Figs 7-8), by which they open into the intestine. At the same level (the junction of the mid and the hind-gut) in the medio-dorsal plane, opens a short and relatively thin Malpighian tubule (Figs 6-10), which has its own, small ampulla. This tubule follows a sinuous line along the hind-gut. It is oriented towards the posterior extremity of the body. The dorsal Malpighian tubule has the distal extremity blindening. The histological structure of the dorsal Malpighian tubule is similar to that of the main lateral Malpighian tubules (Fig. 6). The epithelium of the tubule is of cuboid shaped cells with brush borders.



Source : MNHN, Paris

The dorso-ventral Malpighian tubules of *S. coleoptrata* show a similar histological structure. Examination of the serial sections of the contact zone between the mid and hind-gut in many species of Lithobiomorpha, Scolopendromorpha and Geophilomorpha confirmed the presence of the main pair of bilaterally-inserted Malpighian tubules. We never found Malpighian tubules with a dorsal or ventral insertion in any representatives of these orders.

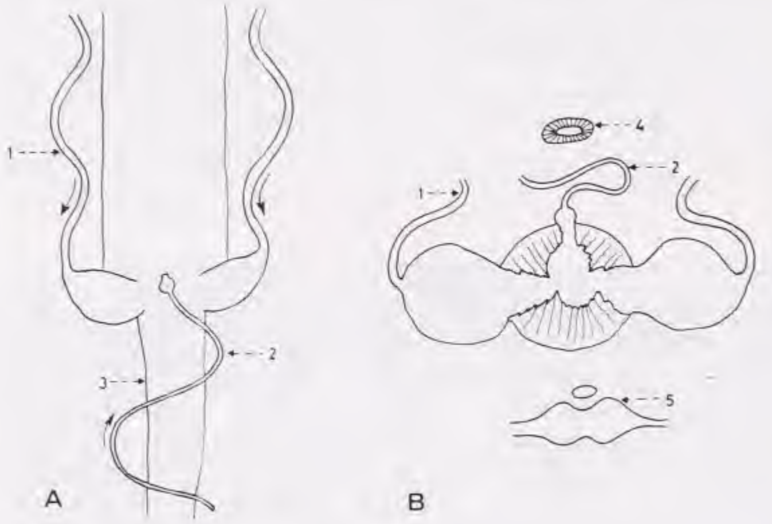


FIG. 10. — Schematic representation of the insertion of the Malpighian tubules of *C. tasmanianus*.
A: dorsal view;
B: transverse section;
1: lateral Malpighian tubule;
2: dorsal Malpighian tubule;
3: hind-gut;
4: vas dorsalis;
5: ventral nerve ganglion.

DISCUSSION

This work does not present data concerning the function of the Malpighian tubules with a dorso-ventral or ventral insertion. Sections through these Malpighian tubules show a similar histological structure to those with a lateral insertion (PALM, 1953; BERTHEAU, 1971).

The presence of a pair of Malpighian tubules with dorso-ventral insertions in *S. coleoptrata* suggests that this feature could represent a plesiomorphic character (PRUNESCU, this volume).

Since, during evolution, different systems and organs in Chilopoda have become simpler, the existence of four Malpighian tubules, in an order which present numerous plesiomorphic characters, may be considered as a plesiomorphic feature. The disappearance of the dorso-ventral Malpighian tubules in the more evolved groups may be considered as an apomorphic feature.

C. tasmanianus represents the archetype of the epimorphic Chilopoda, meaning that their ancestor presented many of the subsequent features of epimorphic Chilopoda. The presence, in this primitive type, of a Malpighian tubule homologous to the dorsal Malpighian tubule in Scutigeromorpha, confirms the plesiomorphic nature of this supernumerary tubule.

REFERENCES

BERTHEAU, P., 1971. — Histologie comparée des tubes de Malpighi de quelques Chilopodes (Myriapodes). *C. R. Acad. Sci., Paris*, **272** : 2913-2915.

LEWIS, J. G. E., 1981. — *The biology of Centipedes*. Cambridge, Cambridge, Univ. Press, 475 pp.

PALM, N. B., 1953. — The elimination of injected vital dyes from the blood in Myriapods. *Ark. Zool., Ser. 2*, **6** : 219-246.

Source : MNHN, Paris

The Structure and Possible Function of the Spiracles of some Scolopendridae (Chilopoda, Scolopendromorpha)

*John G. E. LEWIS *, Trevor J. HILL * & Gavin E. WAKLEY ***

* Taunton School, Taunton, Somerset TA2 6AD, U. K.
** Department of Biological Sciences, Washington Singer Laboratories, University of Exeter, Perry Road, Exeter EX4 4QG, U. K.

ABSTRACT

The results of a scanning electron microscope investigation into the structure of the spiracles of four species of scolopendrid centipedes are reported. *Rhysida nuda togoensis* (Kraepelin), *Ethmostigmus trigonopodus* (Leach), *Scolopendra morsitans* L., *Scolopendra valida* Lucas, were studied. The spiracles serve to prevent debris entering the tracheal system. The relatively simple spiracles of *Rhysida* and *Ethmostigmus* may function as a plastron in small specimens. The more complex spiracles of *Scolopendra* spp. may function principally to prevent water loss, although it is possible that the large sub-atrial cavities in *S. morsitans* may form a plastron. *R. nuda* and *E. trigonopodus* are absent from arid habitats.

RÉSUMÉ

Structure et fonction probable des spiracles de quelques Scolopendridae (Chilopoda, Scolopendromorpha).

L'ultrastructure des spiracles de Scolopendridae est étudiée chez *Rhysida nuda togoensis* (Kraepelin), *Ethmostigmus trigonopodus* (Leach), *Scolopendra morsitans* L., et *Scolopendra valida* Lucas. La fonction des spiracles est essentiellement d'empêcher l'entrée de débris dans le système trachéen. Ils sont simples chez *Rhysida* et *Ethmostigmus*, qui manquent dans les habitats arides, et fonctionnent comme plastron chez les petits individus. Plus complexes chez *Scolopendra* sp., ils pourraient fonctionner comme préventifs du dessèchement, bien qu'il soit possible que la grande cavité sous-atriale de *S. morsitans* forme un plastron.

INTRODUCTION

The literature on the structure of centipede spiracles has been reviewed by VERHOEFF (1941) and LEWIS (1981). Most genera of the order Scolopendromorpha have 21 leg-bearing segments and in these spiracles are present on segments 3, 5, 8, 10, 12, 14, 16, 18 and 20 and sometimes 7.

In genera with 23 leg-bearing segments spiracles are, in addition, present on segment 22. The genus *Plutonium* is unusual in having spiracles on every leg-bearing segment except the first and last.

The scolopendromorphs show a considerable variation in spiracle structure. In the family Cryptopsidae the elliptical spiracle in *Cryptops* leads to the atrium which itself opens by a

---

LEWIS, J. G. E., HILL, T. J. & WAKLEY, G. E., 1996. — The structure and possible function of the spiracles of some Scolopendridae (Chilopoda, Scolopendromorpha). *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 441-449. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

crescent-shaped slit into a subatrial cavity (FÜLLER, 1960): both cavities are lined by trichomes. In *Otocryptops* the atrium is funnel-shaped and there is no subatrial cavity (VERHOEFF, 1941). The two subfamilies of the Scolopendridae are distinguished by the structure of their spiracles. In the Otostigminae the spiracles are mostly rounded and without valves (Fig. 1A) whereas the Scolopendrinae have triangular spiracles with three-flapped valves (Fig. 3A).

MATERIALS AND METHODS

Four species have been investigated using the scanning electron microscope, namely: *Rhysida nuda togoensis* Kraepelin, *Ethmostigmus trigonopodus* (Leach) and *Scolopendra morsitans* L., all from Nigeria, and *Scolopendra valida* Lucas from Oman.

The material, which had been preserved in 70 per cent ethanol, was dehydrated in absolute ethanol for at least 24 hours and then air dried, sputter coated with gold and then examined in a Cambridge 100S scanning electron microscope. Preparations for examination under the light microscope were mounted in Hoyer's mountant.

RESULTS

Subfamily Otostigminae

Rhysida nuda togoensis Kraepelin

The spiracles of *Rhysida* are approximately elliptical (Fig. 1A), the axis of the ellipse sloping obliquely forwards and upwards on segment 3 but more or less vertical on the posterior spiracles, the lower border less curved than the upper. The first spiracle, is almost twice the length of the subsequent ones. The peritrema is scalloped. The atrial wall is thrown into a number of vertical ridges and the floor into humps (Fig. 1B, C). The atrial surface is covered by complex trichomes which are of variable shape. Those immediately beneath the peritrema have angular heads but most are elongated. The sides show a reticulate strutting so that they are honey-combed with cavities (Fig. 1D). The ridge-like trichomes are 11 µm high, 10-14 µm long and 1.25-2.50 µm wide. The wide tracheae open between the humps of the atrial floor. Their openings are surrounded by digitate trichomes whose surfaces are covered by a network of ridges (Fig. 1E). They are 60 µm long and are here termed guard hairs.

Ethmostigmus trigonopodus (Leach)

The general structure of the spiracle of *Ethmostigmus (=Heterostoma)* was accurately described by HAASE (1884) and by VERHOEFF (1941). As in *Rhysida* the spiracles are approximately elliptical but the first spiracle (Fig. 2A) is particularly large and the atrium saucer-shaped, its floor being only slightly below the level the surrounding stigmatopleurite (Fig. 5A). The subsequent spiracles become progressively more bowl-like and in small specimens resemble those of *Rhysida*. The floor of the spiracle (Fig. 2B) is thrown into large humps or ridges covered with trichomes. Those on top of the humps have scalloped heads 7-12 µm across (Fig. 2C). These were described as six-pointed stars by VERHOEFF. The sides and bases show reticulate strutting (Fig. 2E). The trichomes become more elongated towards the base of the humps so that they resemble those of *Rhysida*. The narrow trichomes are 9-11.4 µm long, 1.4-1.8 µm wide and 10 µm high. The tracheae open at the bases of the humps, their openings protected, as in *Rhysida*, by elongated guard hairs 64 µm long (Fig. 2D, E).

Subfamily Scolopendrinae

Scolopendra morsitans Linnaeus

The structure of the spiracle is very similar to that described for *S. cingulata* Latreille by HAASE (1884) and CHALANDE (1885). It is triangular, the apex being anterior (Fig. 3A). The peritrema is scalloped, most lobes having a short seta centrally.

Source : MNHN, Paris

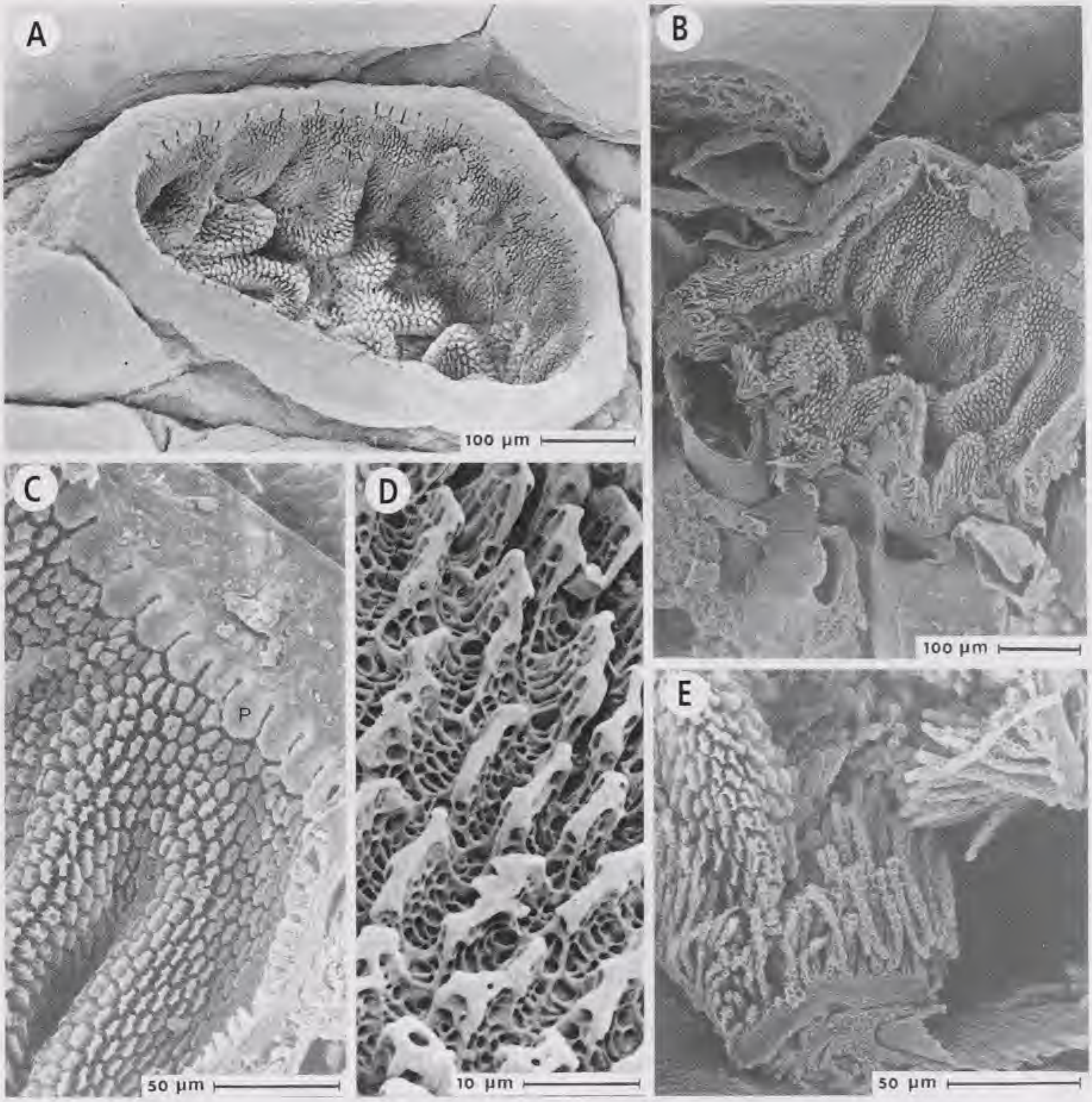


FIG. 1. — *Rhysida nuda togoensis*. Spiracle of segment 3. A. Surface view. B. Vertical section. C. Detail of wall of atrium. P, peritrema. D. Atrial trichomes. E. Guard hairs of tracheal openings.

The atrium is divided into outer and inner cavities by a three flapped valve (Fig. 3B, 5B). The inner atrial cavity is often termed the sub-atrial cavity. Beneath the peritrema the atrial wall bears ridged columnar trichomes 8 μm high, these increase in length towards the valves (Fig. 3D). At the base of the outer atrial cavity there is a row of setose cones (CHALANDE's recumbent plumes) pointing vertically towards the opening of the spiracle (Fig. 3B, C). On the spiracle of segment three there are 8 on the posterior valve and 21-22 on the dorsal and ventral valves. They are about 100 μm high and the longest setae or bristles are 41 μm long. They fill much of the

Source : MNHN, Paris

outer atrial cavity, having but a narrow Y-shaped aperture between them. Beneath the row of cones is a band of vertically ridged cuticle devoid of trichomes which forms a valve. The subatrial cavity is extensive, with deeply folded walls covered with trichomes (Fig. 5B). These are 4.6 µm high, their irregularly pitted heads measuring about 6 µm across. The sides show reticulate strutting which is continued on the atrial floor between the trichomes (Fig. 3E). The tracheae open into the floor and sides of the inner atrial cavity, their openings being surrounded by guard hairs like those of *Rhysida* and *Ethmostigmus* (Fig. 3F). These are about 40 µm long.

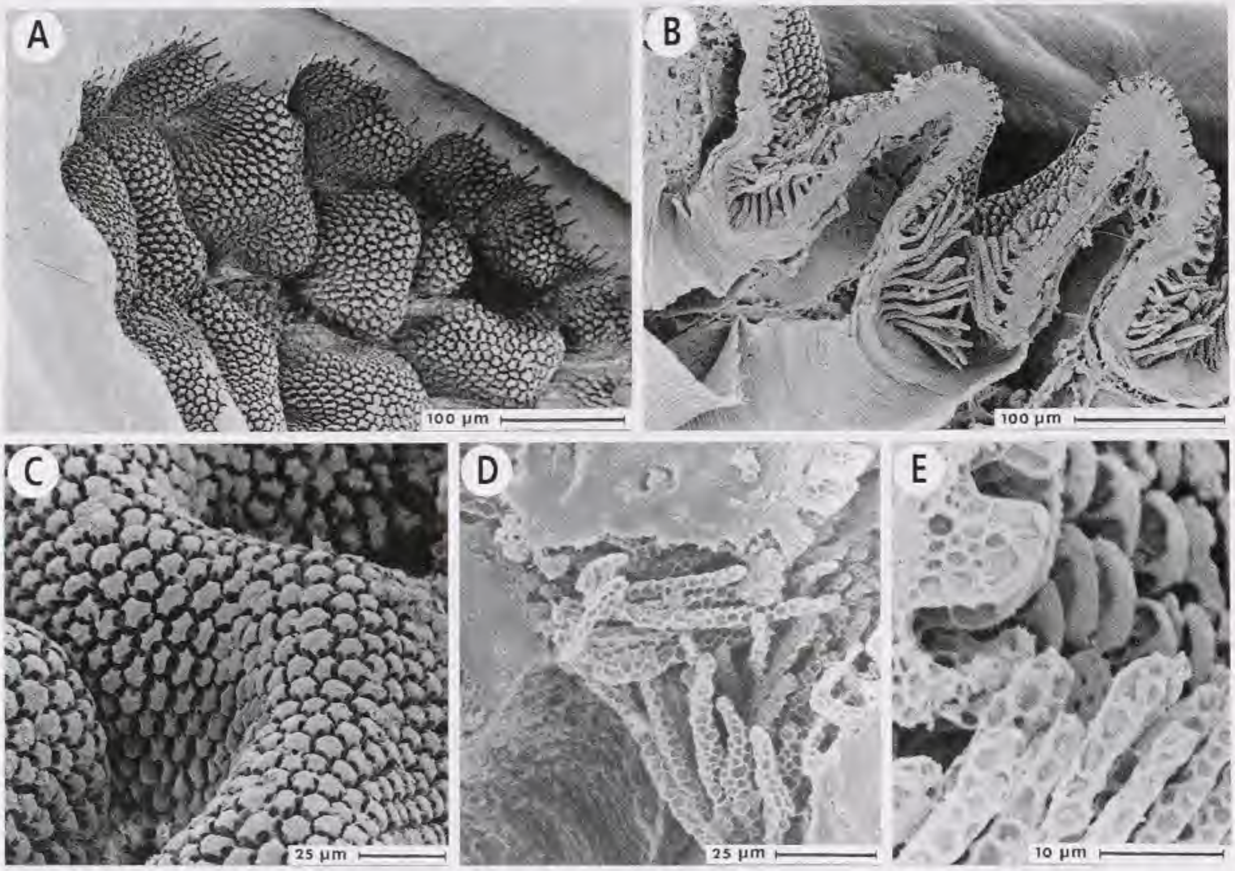


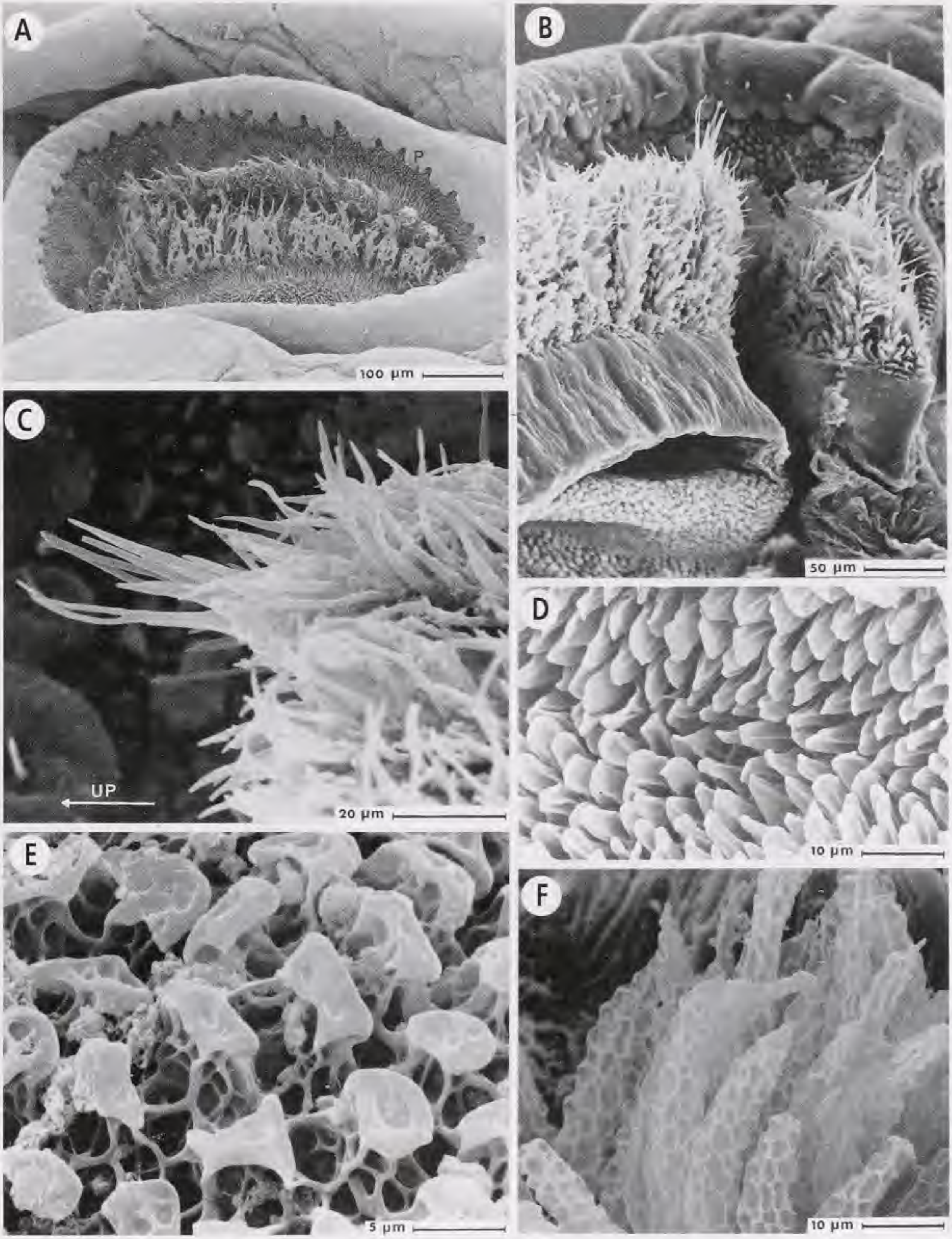
FIG. 2. — *Ethmostigmus trigonopodus*. Spiracle of segment 3. A. Surface view. B. Vertical section (detail). C. Surface view of atrial trichomes. D. Guard hairs of tracheal opening. E. Detail of guard hairs and trichomes.

Scolopendra valida Lucas

The spiracle of *S. valida* (Fig. 4A) resembles that of *S. morsitans* in shape and its division into an outer and inner atrial cavity. The wall of the outer atrial cavity bears trichomes similar to those of *S. morsitans* (Fig. 4B, C). The setae are, however, not borne on cones but form a dense strip along the top of each valve. The valves are composed of trichome free cuticle (Fig. 4D). The inner atrial cavity is not enlarged like that of *S. morsitans* and lacks trichomes. The tracheae open into the chamber, their openings being surrounded by guard hairs 60 µm long.

FIG. 3. — *Scolopendra morsitans*. Spiracle of segment 3. A. Surface view. B. Vertical longitudinal section. C. Setose cone. D. Trichomes of outer atrial cavity. E. Trichomes of inner atrial cavity. F. Guard hairs.

Source : MNHN, Paris



Source : MNHN, Paris

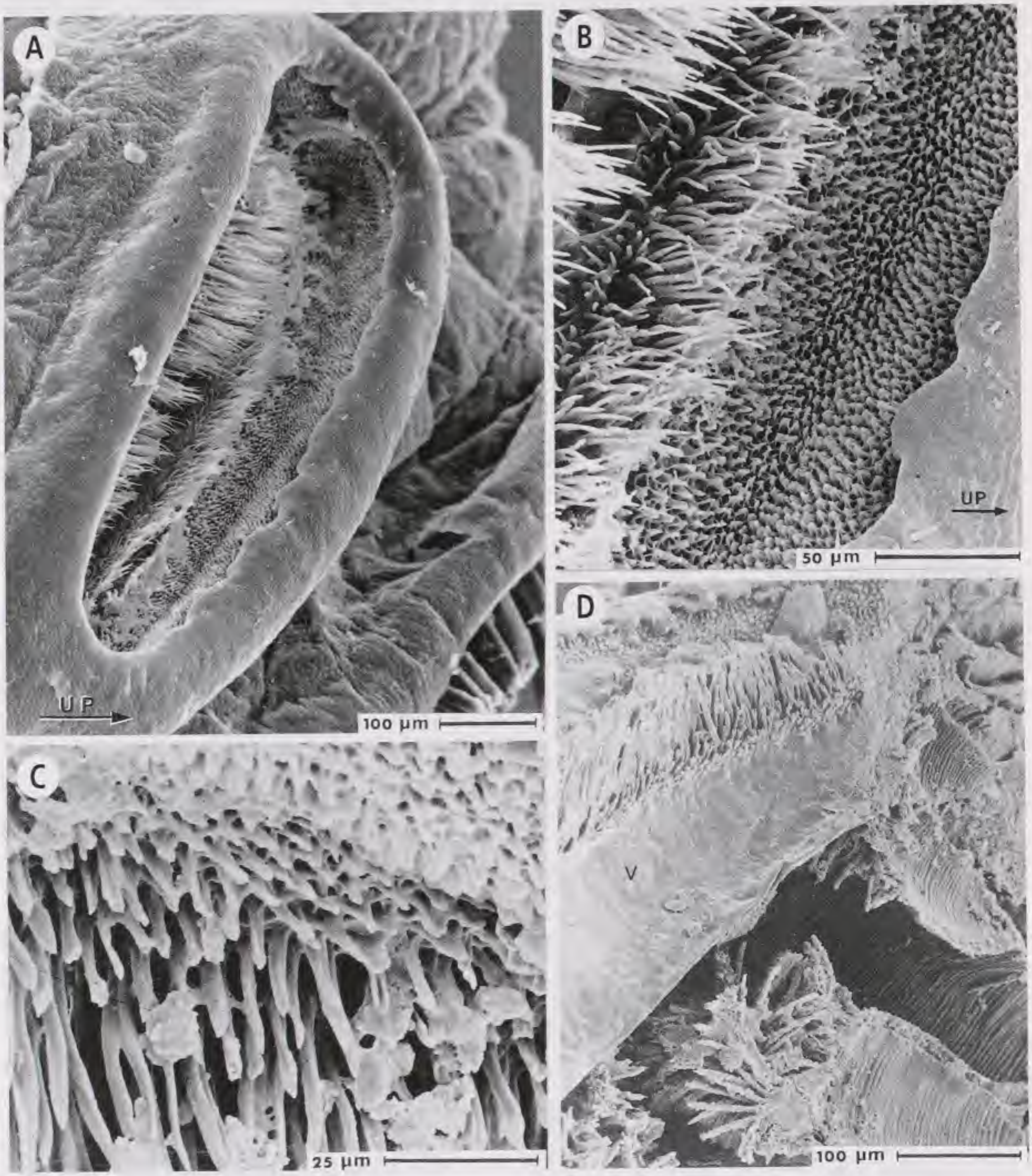


FIG. 4. — *Scolopendra valida*. Spiracle of segment 3. A. Surface view. B. Atrial trichomes and setae. C. Detail trichomes. D. Vertical longitudinal section. V, valve.

Source : MNHN, Paris

DISCUSSION

Spiracles function to reduce water loss from the tracheal system under dry conditions and, in arthropods that experience immersion in water, they frequently act as plastrons. The trichomes may be involved in both these processes. Other functions that have been suggested for spiracular trichomes are that they filter out dust (KAUFMANN, 1962) and prevent spiracular occlusion during locomotion (CURRY, 1974). PUGH *et al.* (1991) suggested that the peritreme of holothyrid mites might prevent suffocation during immersion or act as a water trap.

Spiracular function in Otostigminae

Water loss from the tracheal openings of *Rhysida* and *Ethmostigmus* may be impeded by the spiracular guard hairs which will also prevent debris entering the tracheae. The crevices between the humps of the atrial floor will also retain humid air. It is difficult to visualise a role for the trichomes in this respect as gases diffusing in and out of the tracheae will pass over them rather than between them. A more likely function is that they form a plastron, retaining a layer of air when the centipede is immersed in water as may happen during the rainy season.

HINTON (1968) determined the basal limit of plastron efficiency for insects in terms of the ratio between the area of the plastron and the wet body weight as 1.5×10^4 $\mu m^2.mg^{-1}$. Assuming that the air-water interface is across the tops of the trichomes, a conservative estimate for this ratio for a large specimen of *R. nuda togoensis* length 74 mm, mass 1080 mg is 3.75×10^3 $\mu m^2.mg^{-1}$: well below HINTON's figure. For a small specimen body length 13 mm, mass 11 mg the figure is 1.5×10^4 $\mu m^2.mg^{-1}$, equal to HINTON's minimum value. In an *E. trigonopodus* length 88 mm, mass 2700 mg the ratio is 4.2×10^3 $\mu m^2.mg^{-1}$ but in a small specimen length 29.5 mm, mass 91 mg the value is 2.2×10^4 $\mu m^2.mg^{-1}$. It would appear that in both species small but not large specimens may be able to utilise plastron respiration. These calculations assume that the interface is across the tops of the trichomes.

Although the relative area of a plastron decreases with increased mass of the organism, tracheal volume will increase in proportion to increasing mass. The tracheae of large specimens appear to be particularly voluminous and may function as air stores during immersion.

Spiracular function in Scolopendrinae

It is tempting to suggest that the greater complexity of the scolopendrine spiracle, with the atrium divided horizontally by a three-flapped valve and the presence in *Scolopendra* spp. of dense setae above the valves either borne on cones or not, is related to the need to restrict water loss in dry conditions. PUGH *et al.* (1987) described structures similar to the setose cones from the peritrematic groove of the mite *Phaulodinychus repleta* (Berlese). They consist of micropapillae arranged on christmas tree-like structures and termed compound fimbriae. They suggested that the compound fimbriae of *P. repleta* carried out a protective function preventing the entry of foreign/harmful material into the tracheal system rather than supporting an air film. The irregular and spiky compound fimbriae of *Holothyrus coccinella* (Wormersley) cannot support an airfilm but would pierce the air water interface (PUGH *et al.*, 1991). The setae of the setose cones of *S. morsitans* and the setae of *S. valida* clearly act as sieves and are often covered with debris. The setae will clearly reduce diffusion. If their surface is not hydrophobe then dipole-dipole interactions between water molecules and the protein and chitin molecules of the cuticle will allow free diffusion of oxygen and carbon dioxide whilst impeding that of water. The spiracles of the *Scolopendra* species are small and the area covered by trichomes in the atrial cavities is low. The ratio between the area and body mass for a *S. morsitans* length 70 mm, mass 1042 mg is 1.6×10^3 $\mu m^2.mg^{-1}$, lc. An order of magnitude below HINTON's figure. The figure for a *S. valida* length 110 mm, mass 4370 mg is even lower: 3.7×10^2 $\mu m^2.mg^{-1}$. *S. morsitans*, though not *S. valida*, has large sub-atrial cavities lined with trichomes (Fig. 5B). If

Source : MNHN, Paris

these were flooded with water it is possible that they would act as a plastron. Currently, however, there are insufficient data to calculate the area involved.

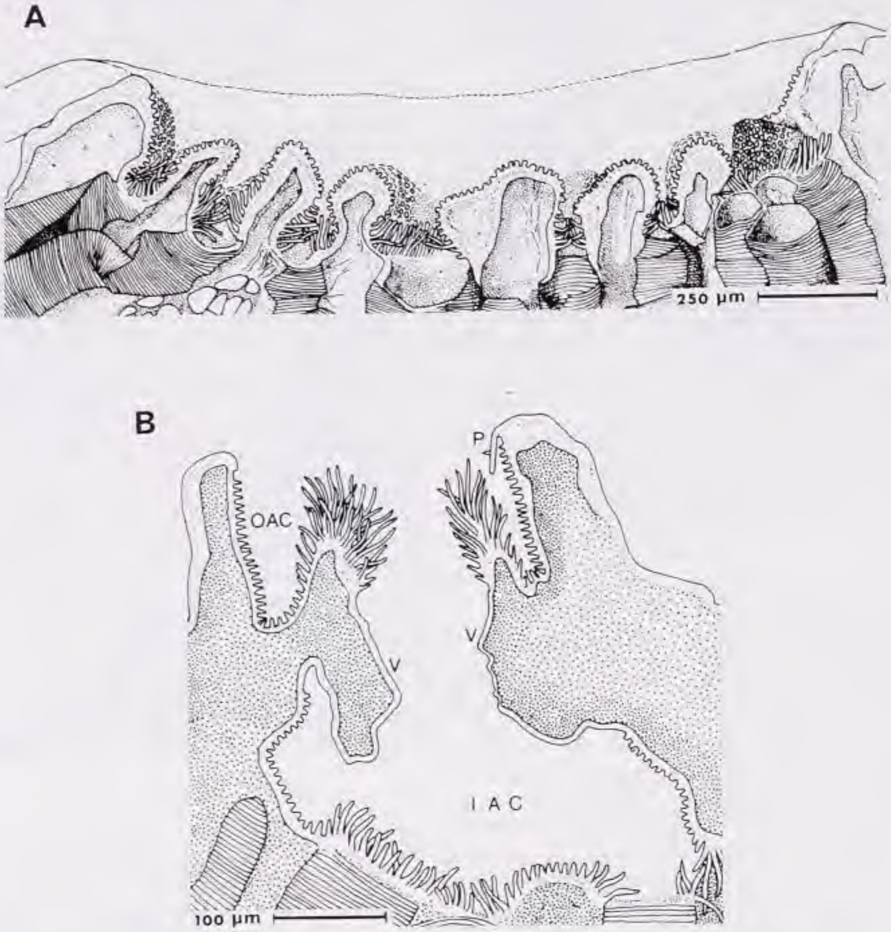


FIG. 5. — A. Vertical longitudinal section of spiracle of segment 3 of *Ethmostigmus trigonopodus*. B. Vertical transverse section of spiracle of segment 3 of *Scolopendra morsitans*. IAC, inner atrial cavity; OAC, outer atrial cavity; P, peritrema; V, valve.

Ecology

Data on the distribution of scolopendrids in West Africa and Saudi Arabia shows that members of the subfamily Scolopendrinae with their triangular spiracles occur in dry and humid regions, whereas members of the subfamily Otostigminae are absent from drier habitats. Thus *Rhysida nuda togoensis* and *Ethmostigmus trigonopodus* are virtually absent from the dry Sudan and Sahel savanna regions of Nigeria (LEWIS, 1972) whereas the scolopendrines *Asanada socotrana* Pocock and *S. morsitans* are widespread there (LEWIS, 1973 and unpublished data).

Rhysida and *Ethmostigmus* have not been recorded from Saudi Arabia but *A. socotrana* and three species of *Scolopendra* (*canidens* Newport, *mirabilis* (Porat) and *valida* Lucas) occur there (LEWIS, 1986).

In the guinea savanna region of Northern Nigeria, *R. nuda* and *E.trigonopodus* are virtually absent from surface habitats during the latter part of the dry season (mid-November to

Source : MNHN, Paris

April) but *S. morsitans* is surface active throughout the year being found under cow dung during the dry season (LEWIS, 1969). The ecological data support the conclusions drawn about possible spiracular functions on the basis of morphological observations.

ACKNOWLEDGMENTS

This work was carried out between 1990 and 1993 with a series of sixth form pupils from Taunton School. The major participants were Susan BADLEY, Tom BASHER, Tom BLANDFORD, Nicola IRVIN, Helen JEWELL, Katie NEWBOLD, Philip SMITH, Robert TUDOR and Paul YEUNG. It was supported by generous grants to J. G. E.LEWIS from the Royal Society and the Association for Science Education Research in Schools Committee which are gratefully acknowledged. J.G.E.LEWIS's thanks are also due to Dr D. J. STRADLING of Exeter University for continued advice and support which are much appreciated. Professor J. A. BRYANT and Dr M. R. MCNAIR kindly allowed us to use the SEM facilities in the Washington Singer Laboratories.

REFERENCES

CHALANDE, J., 1885. — Recherches anatomiques sur l'appareil respiratoire chez les chilopodes de France. *Bull. Soc. Hist. nat. Toulouse*, **19** : 39-66.

CURRY, A., 1974. — The spiracle structure and resistance to desiccation of centipedes. *Symp. zool. Soc. Lond.* , **32** : 365-382.

FÜLLER, H., 1960. — Untersuchungen über den Bau der Stigmen bei Chilopoden. *Zool. Jb. (Anat.)*, **78** : 129-144.

HAASE, E., 1884. — Das Respirationssystem der Symphylen und Chilopoden. *Zool. Beitr.*, **1** : 65-96.

HINTON, H. E., 1968. — Spiracular gills. *Adv. Insect Physiol.*, **126** : 65-162.

KAUFMAN, Z. S., 1962. — The structure and development of stigmata in *Lithobius forficatus* L. (Chilopoda, Lithobiidae). *Ent. Obozr.*, **41** : 223-225. (In Russian with English summary).

LEWIS, J. G. E., 1969 (70). — The biology of *Scolopendra amazonica* in Nigerian Guinea savannah. *Bull. Mus. natl. Hist. nat., Paris*, **41, suppl. n°2** : 85-90.

LEWIS, J. G. E., 1972. — The life histories and distribution of the centipedes *Rhysida nuda togoensis* and *Ethmostigmus trigonopodus* (Scolopendromorpha, Scolopendridae) in Nigeria. *J. Zool., Lond.*, **197** : 399-414.

LEWIS, J. G. E., 1973. — The taxonomy, distribution and ecology of centipedes of the genus *Asanada* (Scolopendromorpha, Scolopendridae) in Nigeria. *Zool. J. Linn. Soc.*, **52** : 97-112.

LEWIS, J. G. E., 1981. — *The biology of centipedes*. Cambridge, Cambridge University Press, 476 pp.

LEWIS, J. G. E., 1986. — Centipedes of Saudi Arabia. *Fauna of Saudi Arabia*, **8** : 20-30.

PUGH, P. J. A., KING, P. E. & FORDY, M. R., 1987. — Structural features associated with respiration in some intertidal Uropodina (Acarina: Mesostigmata). *J. Zool., Lond.*, **211** : 107-120.

PUGH, P. J. A., EVANS, G. O., KING, P. E. & FORDY, M. R. & King, P. E., 1991. — The functional morphology of the respiratory system of the Holothyrida (=Tetrastigmata) (Acari: Anactinotrichida). *J. Zool., Lond.*, **225** : 153-172.

VERHOEFF, K. W., 1941. — Zur Kenntnis der Chilopodenstigmen. *Z. Morph. Ökol. Tiere.*, **38** : 96-117.

Source : MNHN, Paris

Source : MNHN, Paris

Population Metabolism of Millipedes at Two Altitudinal Zones in the Central Alps (Tirol, Austria)

Erwin MEYER, *Peter* MARSONER & *Elisabeth* FISCHER

Institute of Zoology, University of Innsbruck
Technikerstr. 25, A-6020 Innsbruck, Austria

ABSTRACT

The respiratory metabolism of *Enantiulus nanus* (LATZEL, 1884) from a mixed oak wood (670 m a.s.l.) and of 3 subalpine species, *Leptoiulus saltuvagus* (Verhoeff, 1898), *Ochogona caroli* (Rothenbühler, 1900) and *Haasea fonticulorum* (Verhoeff, 1910) from an *Alnus viridis* community (2000 m) was measured using a Gilson respirometer and a Warburg respirometer with electronic manometers. Temperature (6-20°C) and mass-specific (*E. n.*: 2-17 mgfw; *L. s.*: 3-75 mgfw; *O. c.*: 1-10 mgfw; *H. f.*: 2-12 mgfw) oxygen consumption values of these species are presented. The lowland species has its greatest sensitivity to temperature changes between 10°C and 15°C, the subalpine species between 6°C and 10°C with Q_{10}-values between 3.1 and 7.9. Based on a mean *E. nanus*-biomass of 2.9 g fresh mass per m^2 (= 73% of the total millipede-biomass) in the oak wood, the population metabolism of this species equalled 1488 ml O_2 m^{-1} and year (= 30 KJ). In contrast a total millipede biomass of 2.2 g fresh mass per m^2 in the subalpine site respires only 732 ml O_2 m^{-1} and year (= 15 KJ). The most important single factor in determining the metabolism for field populations is its population structure and biomass.

RÉSUMÉ

Métabolisme de populations de diplopodes dans deux zones altitudinales des Alpes Centrales (Tyrol, Autriche).

Le métabolisme respiratoire de *Enantiulus nanus* (Latzel, 1884) d'une forêt mixte de chêne (altitude 670 m) et de trois espèces subalpines, *Leptoiulus saltuvagus* (Verhoeff, 1898), *Ochogona caroli* (Rothenbühler, 1900) et *Haasea fonticulorum* (Verhoeff, 1910) d'un peuplement à *Alnus viridis* (altitude 2000 m) a été mesuré à l'aide d'un respiromètre de type Gilson et d'un respiromètre de type Warburg équipés de manomètres électroniques. On donne ici les températures (6-20°C), les masses spécifiques fraîches (*E. n.* : 2-17 mg mf; *L. s.* : 3-75 mg mf; *H. f.* : 2-12 mg mf) et les valeurs respectives de consommation en oxygène. L'espèce de plaine présente une plus grande sensibilité aux changements de température entre 10°C et 15°C, les espèces alpines entre 6°C et 10°C, avec des valeurs de Q_{10} variant de 3,1 à 7,9. En se basant sur une biomasse moyenne pour *E. nanus* égale à 2,9 grammes de matière fraîche par mètre carré (qui représente 73% de la biomasse totale des diplopodes) dans la chênaie, le métabolisme respiratoire annuel de cette population équivaut à 1488 ml O_2 m^{-1} (= 30 KJ). En comparaison, une biomasse totale de diplopodes de 2,2 g de matière fraîche par mètre carré ne représente, dans les sites subalpins, qu'une respiration de 732 ml O_2 m^{-1} (= 15 KJ). Le facteur le plus important dans le déterminisme du métabolisme respiratoire des populations sur le terrain semble être la structure du peuplement et la biomasse.

MEYER, E., MARSONER, P. & FISCHER, E., 1996. — Population metabolism of millipedes at two altitudinal zones in the Central Alps (Tirol, Austria). *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 451-460. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

INTRODUCTION

In a recent contribution PENTEADO *et al.* (1991) have summarized available data on oxygen consumption in millipedes. Respiratory rates of more than 20 species living in temperate or tropical regions, ranging in size from 10 to 4000 mg have been evaluated and discussed in relation to size of individual and sex. Further variables such as temperature, life stages or decreased oxygen tension have been investigated in numerous papers such as DWARAKANATH (1971), GROMYSZ-KALKOWSKA (1970, 1973), GROMYSZ-KALKOWSKA & STOJALOWSKA (1966) or PENTEADO & HEBLING-BERALDO (1991). Data on oxygen consumption rates of millipedes in context with the life-cycle and population structure are rare. WOOTEN & CRAWFORD (1974) gave such an example by combining monthly measurements of the respiration rate of a desert millipede with its behaviour in the field.

The aim of the present paper is to combine detailed laboratory investigations of the respiratory rates of four alpine millipede species (FISCHER, 1985; MARSONER, 1992) with the results from studies on the population structure, life-cycle and temperatures in their habitats (MEYER, 1979, 1985; KOFLER & MEYER, 1992). In this way it is possible to evaluate the relative importance of variables such as age structure, biomass, time of the year, temperature and altitude affecting the population metabolism in the field.

MATERIAL AND METHODS

Specimens of *Enantiulus nanus* (Latzel) (2-17 mg live mass) were collected from an inneralpine mixed oak wood (670 m a.s.l.) in the Inn-valley near Stams at four occasions between October 1990 and October 1991. The life-history, abundance and production of this species have been studied in detail by KOFLER & MEYER (1992). The annual mean abundance of *E. nanus* is 859 inds m^{-2} and this species dominates the total millipede fauna in this oak wood. Males reach maturity first as stadium VIII in the 3rd year, females also become adult with stage VIII and lay eggs after the third overwintering. This iteroparous julid species shows a seven-year life-cycle. A mean overwintering biomass of 2.9 g fresh mass m^{-2} produces 1.5 g fresh mass m^{-2} $year^{-1}$. The animals were kept in plastic boxes provided with tap water agar to maintain a near 100% humidity and fed dead leaves. These cultures were maintained at field-like conditions with fluctuating temperatures (night/day): March, April and October: 7.5°C/12.5°C, May, June and September: 12.5°C/17.5°C, July and August: 17.5°C/22.5°C, November: 2.5°C/7.5°C. Approximately 470 inds of *E. nanus* were used in the assessment of respiratory metabolism between March and November 1991. Experimental temperatures were: 5°C (November), 10°C (March, April, October), 15°C (May, June, September) and 20°C (July and August). Rates of oxygen uptake of individual specimens were measured using a Warburg respirometer with electronic manometers connected to a module box and a PC. During each experiment 13 respirometer flasks (Volume: 2.2-2.6 ml) contained animals and one acted as a thermo-barometer-control. In each flask CO_2 was absorbed by a 5% solution of NaOH (20 µl) pipetted into the lower part of a two-piece flask. The animals were placed into the upper part of the flask which had a sintered floor to allow gas exchange. A high humidity was maintained by inserting a damp and crumpled piece of filter paper. After introducing the individuals into the flasks an half hour settling period was allowed to elapse before closing the respirometer valves. Each experiment lasted at least 24 h. At the end of the experimental period the millipedes were weighed individually. Oxygen consumption was calculated from a series of usually 144 measurements (10 min measuring intervals) by excluding the first hour (6 measurements) after closing the valves.

Specimens of *Leptoiulus saltuvagus* (Verhoeff) (3-75 mg life mass), *Ochogona caroli* (Rothenbühler) (1-10 mg life mass) and *Haasea fonticulorum* (Verhoeff) (2-12 mg life mass) were collected from an *Alnetum viridis* (2000 m a.s.l.) in the Ötztal Alps near Obergurgl at several occasions between August and October 1984. Previous investigations by MEYER (1979, 1985) established for *L. saltuvagus* a mean density of 209 inds m^{-2} and a biomass 1.2 g fresh mass m^{-2}. The semelparous julid species reaches maturity in stage IX, X or XI after four or five years. At the same site the two chordeumatid species have a mean density of 112 inds m^{-2} (*O. caroli*) and 107 inds m^{-2} (*H. fonticulorum*). This corresponds with a mean biomass of 0.42 g fresh mass m^{-2} (*O. c.*) and 0.63 g fresh mass m^{-2} (*H. f.*). A three-year life-cycle is probable for both chordeumatid species.

The animals were kept in light-temperature chambers representing approximately field conditions (day/night-temperature: 12°C/8°C, 12/12 h) in plastic boxes provided with tap water agar to maintain a near 100% humidity and fed dead leaves. Approximately 80 individuals of *L. saltuvagus* and 40 individuals each of *O. caroli* and *H. fonticulorum* were used in the assessment of respiratory metabolism. Between July 1984 and February 1985 rates of oxygen uptake of individual specimens of the three species were measured using a refrigerated GR-14 Gilson differential respirometer. Measurements were made at 6°C, 10°C, 15°C and 20°C. During each experiment 9-12 respirometer flasks (Volume: 25 ml) contained animals and three acted as controls. In each flask CO_2 was absorbed by 5N NaOH pipetted onto a roll of filter paper held in the centre well. A perforated plastic cylinder placed over the central wall prevented the animals making contact with the NaOH. A high humidity was maintained with moist filter paper on the floor of the chamber. Two damp

Source : MNHN, Paris

and crumpled 1 cm^2 pieces of the same material provided shelter and the animals usually became quiescent within 1 h of being placed in the vessels. Because of the respirometer response and precision, 3 individuals of the smallest size classes were placed in each chamber.

Temperatures in the litter layer of the two sites were recorded with a Goerz Thermoscript (clockwork mechanism and bimetallic probe).

RESULTS

The relationship between respiratory rate and size of individual

Enantiulus nanus (Latzel, 1884)

As indicated in Table 1, the smallest specimens of *E. nanus* consume at least twice as much oxygen per unit mass than the largest ones at all experimental temperatures between 5°C and 20°C. The b-values according to the equation $R = a W^b$ where R is the respiratory rate expressed in µl oxygen ind^{-1} are scattered between 0.012 (5°C, Nov.), 0.205 (10°C, Oct.), 0.236 (15°C, June), 0.306 (20°C, Aug.), 0.329 (15°C, May), 0.441 (15°C, Sept.) and 0.488 (20°C, July) depending on temperature and time of the year.

TABLE 1. — Mean ($\bar{x}$±S.E.) rates of oxygen consumption per unit mass (µl mg^{-1} h^{-1}) over the size range of *Enantiulus nanus* at 5°C, 10°C, 15°C and 20°C.

Size range (mg)	n	5°C	n	10°C	n	15°C	n	20°C
1.6 - 4.9	6	0.09±0.01	6	0.13±0.03	11	0.21±0.03	4	0.22±0.03
5.0 - 6.9	4	0.05±0.01	12	0.08±0.01	30	0.14±0.01	17	0.14±0.01
7.0 - 10.9	11	0.04±0.01	25	0.06±0.01	43	0.11±0.01	19	0.12±0.01
11.0 - 16.6	4	0.03±0.01	13	0.05±0.01	33	0.08±0.01	16	0.10±0.01

Leptoiulus saltuvagus (Verhoeff, 1898)

Table 2 shows the respiratory rates of *L. saltuvagus*. Again juveniles consume considerably more oxygen per unit mass than adults. The calculated b-values are between 0.67 (10°C), 0.68 (20°C), 0.82 (15°C) and 0.92 (6°C).

TABLE 2. — Mean ($\bar{x}$±S.E.) rates of oxygen consumption per unit mass (µl mg^{-1} h^{-1}) over the size range of *Leptoiulus saltuvagus* at 5°C, 10°C, 15°C and 20°C.

Size range (mg)	n	6°C	n	10°C	n	15°C	n	20°C
3.0 - 16.0	6	0.08±0.01	16	0.18±0.01	5	0.21±0.03	7	0.36±0.03
17.4 - 74.8	9	0.07±0.01	14	0.11±0.01	8	0.15±0.01	7	0.21±0.04

Ochogona caroli (Rothenbühler, 1900)

Mass specific oxygen consumption rates of *O. caroli* (Table 3) indicate higher values for juveniles than for adults. Depending on temperature b-values range between 0.60 (6°C), 0.66 (15°C), 0.81 (10°C) and 0.83 (20°C).

TABLE 3. — Mean ($\bar{x}$±S.E.) rates of oxygen consumption per unit mass (µl mg^{-1} h^{-1}) over the size range of *Ochogona caroli* at 5°C, 10°C, 15°C and 20°C.

Size range (mg)	n	6°C	n	10°C	n	15°C	n	20°C
1.2 - 3.2	7	0.16±0.01	5	0.24±0.03	7	0.30±0.06	11	0.32±0.02
5.1 - 10.3	8	0.09±0.01	9	0.17±0.02	9	0.17±0.01	8	0.27±0.04

Source : MNHN, Paris

Haasea fonticulorum (Verhoeff, 1910)

The rates of oxygen consumption per unit mass over the size range of *H. fonticulorum* (Table 4) indicate unexpectedly high values for the adults. Even the calculated b-values ranging between 0.94 (6°C), 1.41 (15° and 20°C) and 1.67 (10°C) do not show the expected relationship between oxgen consumption and size of the individuals. However, the evident activity peak of adult *H. fonticulorum* between September and November known from pitfall trapping (MEYER, 1979) may be responsible for the extraordinary respiration rates as the experiments were carried out between 20th Sept. and 12th Dec.

TABLE 4. — Mean ($\bar{x}$±S.E.) rates of oxygen consumption per unit mass (µl mg^{-1} h^{-1}) over the size range of *Haasea fonticulorum* at 5°C, 10°C, 15°C and 20°C.

Size range (mg)	n	6°C	n	10°C	n	15°C	n	20°C
1.9 - 4.6	3	0.09±0.02	5	0.17±0.05	7	0.19±0.02	3	0.28±0.05
5.4 - 11.8	8	0.10±0.01	8	0.25±0.01	7	0.30±0.02	5	0.45±0.03

The relationship between respiratory rate and temperature

This relationship was investigated using specimens that had been reared at quasi field temperatures throughout the year and measured at corresponding experimental temperatures of 5°C, 10°C, 15°C and 20°C. The results given in Tables 1-4 and Figures 2-5 indicate that oxygen consumption rates of the four species investigated do not gradually increase with increasing temperature. In *E. nanus* the steepest increase in oxygen comsumption takes place between 10°C and 15°C which can be summarised as a Q_{10} value of 3.08 (mean over all size classes). Between 15°C and 20°C the respiratory metabolism is nearly balanced (Q_{10} = 1.21). In the three subalpine species (*L. saltuvagus, O. caroli* and *H. fonticulorum*) the independence of their respiratory metabolism of the temperature lies between 10°C and 15°C. In all cases the Q_{10} values are not significantly different from 1 (MANN-WHITNEY test). Between 6°C and 10°C the relationship between respiratory rate and temperature is very close with Q_{10} values of 7.9 (*L. saltuvagus*), 3.2 (*O. caroli*) and 7.2 (*H. fonticulorum*).

Variation in respiratory rate with season

Measurements of the respiratory metabolism of *E. nanus* were carried out during the period between April and November. The experimental temperatures corresponded to the rearing temperatures and those to the temperature in the litter layer of its habitat. Hence in April and October the experimental temperature was 10°C, in May, June and September 15°C, in July and August 20°C and in November 5°C. In Figure 1, the respiratory rates at corresponding experimental temperatures but different months are compared.

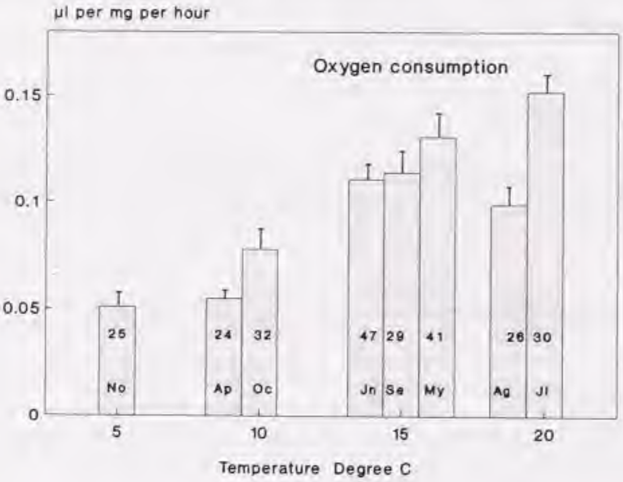


FIG. 1. — Mean ($\bar{x}$ ± S.E.) respiratory rates of *Enantiulus nanus* at different temperatures and seasons. The letters within the columns indicate the month in which the respiration experiments at the given temperature were made. The figures within the columns indicate the number of animals used.

Source : MNHN, Paris

Relating results to the season (months), there is no significant difference in the respiratory rate of *E. nanus* at 10°C and 15°C. Only in August at the given temperature of 20°C did the animals respire at a significantly lower rate than in July. That corresponds with the life cycle of *E. nanus*. Adults undergo their annual moulting phase in August and are therefore inactive.

Estimation of population metabolism

PHILLIPSON (1970) recommended a "best estimate" of respiratory metabolism as the mean energy loss per unit mass per unit time calculated from laboratory measurements on all life stages of a given species. Its calculation is independent of field population data, fluctuations in field temperatures and generation time. During this investigation, oxygen consumption of all life stages of four millipede species has been measured at temperatures of 5°C, 10°C, 15°C and 20°C. The results are summarised in Tables 1-4. Estimates of population metabolism have been obtained by multiplying the size- and temperature- specific respiratory rates with the time- and age- specific biomass data from the field (Figs 2-5). It should be mentioned that the temperature specific respiration rates were calculated on the basis of the Q_{10} values and not on the assumption that respiratory rate is an exponential function of temperature, as was demonstrated by HASSALL (1983) for the isopod *Philoscia muscorum*.

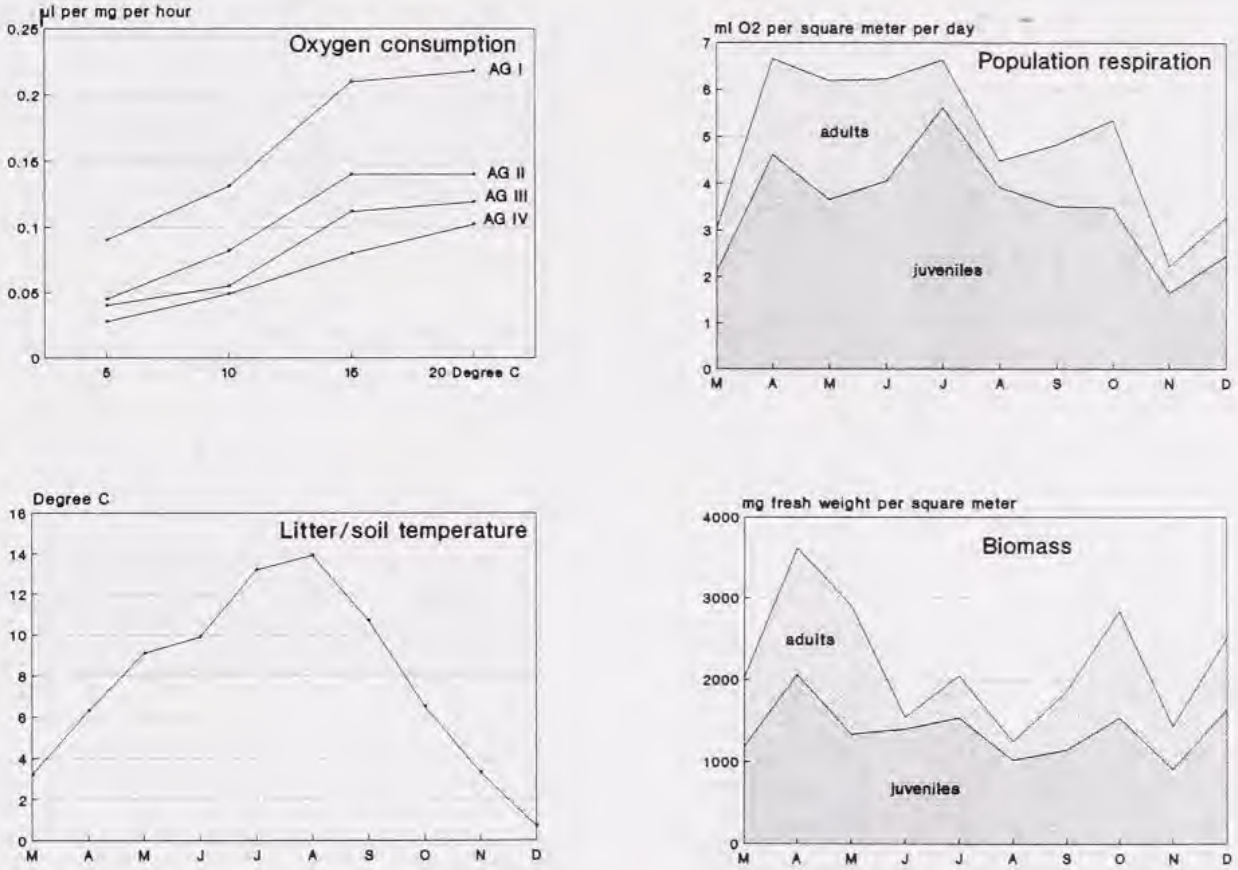


FIG. 2. — Top left: The relationship between oxygen consumption and temperature for the four age groups (AG) of *E. nanus*. The size range of the different groups are given in Table 1. Bottom left: Mean monthly temperature in the litter layer of the oak wood. Bottom right: Mean monthly biomass of juveniles (age group I, stage II-VIII) and adults (age group II - IV, stage IX-XIV) of *E. nanus* in the oak wood (taken from KOFLER & MEYER 1992). Top right: Oxygen consumption by the whole population over the period March-December.

Source : MNHN, Paris

Enantiulus nanus (Latzel, 1884) (Fig. 2)

The sum of estimates for each age group gives a total oxygen consumption of 1488 ml O_2 m^{-1} $year^{-1}$ (= 30 KJ m^{-1}) for the population of *E. nanus* in the oak wood. The graphical presentation of the data provides an impression of the relationships between the field temperatures, the dynamics of the biomass and the population metabolism during the vegetation period. Highest total respiration rates are obtained between April and July. In spite of declining biomass due to the disappearance of adults (but favoured by the rising temperature) the population metabolism stays on the same level in the first half of the year. The second biomass peak during October brings the population metabolism again nearly to the same level. The portion attributable to juvenile metabolism is 59-88% in the total population and it is highest in July and August when the new generation is appearing. Adults show their highest respiration rates in May and June during the egg-laying period.

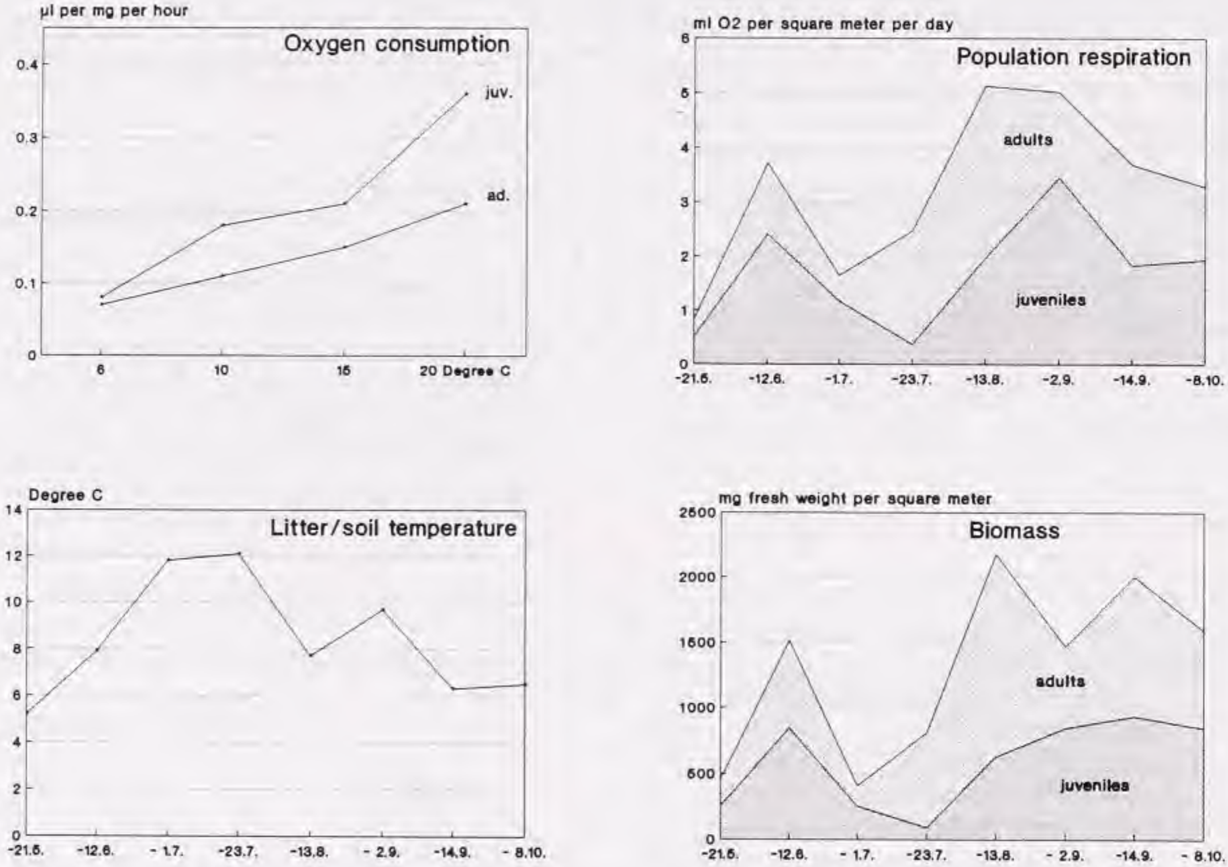


FIG. 3. — Top left: The relationship between oxygen consumption and temperature for juveniles and adults of *L. saltuvagus*. The size range of the two groups are given in Table 2. Bottom left: Mean monthly temperature in the litter layer of the *Alnetum viridis* at 2000 m a.s.l. Bottom right: Mean monthly biomass of juveniles (stage III-VIII) and adults (stage IX-XI) of *L. saltuvagus* in the *Alnetum viridis* (taken from MEYER, 1985). Top right: Oxygen consumption by the whole population over the period May-October.

Leptoiulus saltuvagus (Verhoeff, 1898) (Fig. 3)

For the population of *L. saltuvagus* living in alder litter at the timberline, an annual respiratory metabolism of 528 ml O_2 m^{-1} (= 10.6 kJ m^{-1}) was calculated. According to the fluctuations in biomass, the oxygen consumption is highest in late summer and autumn. The

Source : MNHN, Paris

period with highest litter temperatures (July) does not become apparent in the population metabolism because at that time the population structure undergoes the yearly change. Overwintered adults disappear, overwintered juveniles are probably moulting and the "this-year's" generation has not yet hatched. The portion attributable to juvenile metabolism is 53% in the total population on average with highest values in spring and autumn.

Ochogona caroli (Rothenbühler, 1900) and ***Haasea fonticulorum*** (Verhoeff, 1910) (Figs 4 and 5)

Total population metabolism of these two Chordeumatida is low. (*O. caroli*: 99 ml O_2 m^{-1} year^{-1}, (= 1.9 KJ m^{-1}); *H. fonticulorum*:105 ml O_2 m^{-1} year^{-1} (= 2.1 KJ m^{-1}). In correspondence with the biomass, highest respiratory rates are obtained in September and October when juveniles and adults occur in large numbers. Adults are short-lived and die in the early spring. 78% (79%) of the total population respiration per year is attributable to the juveniles.

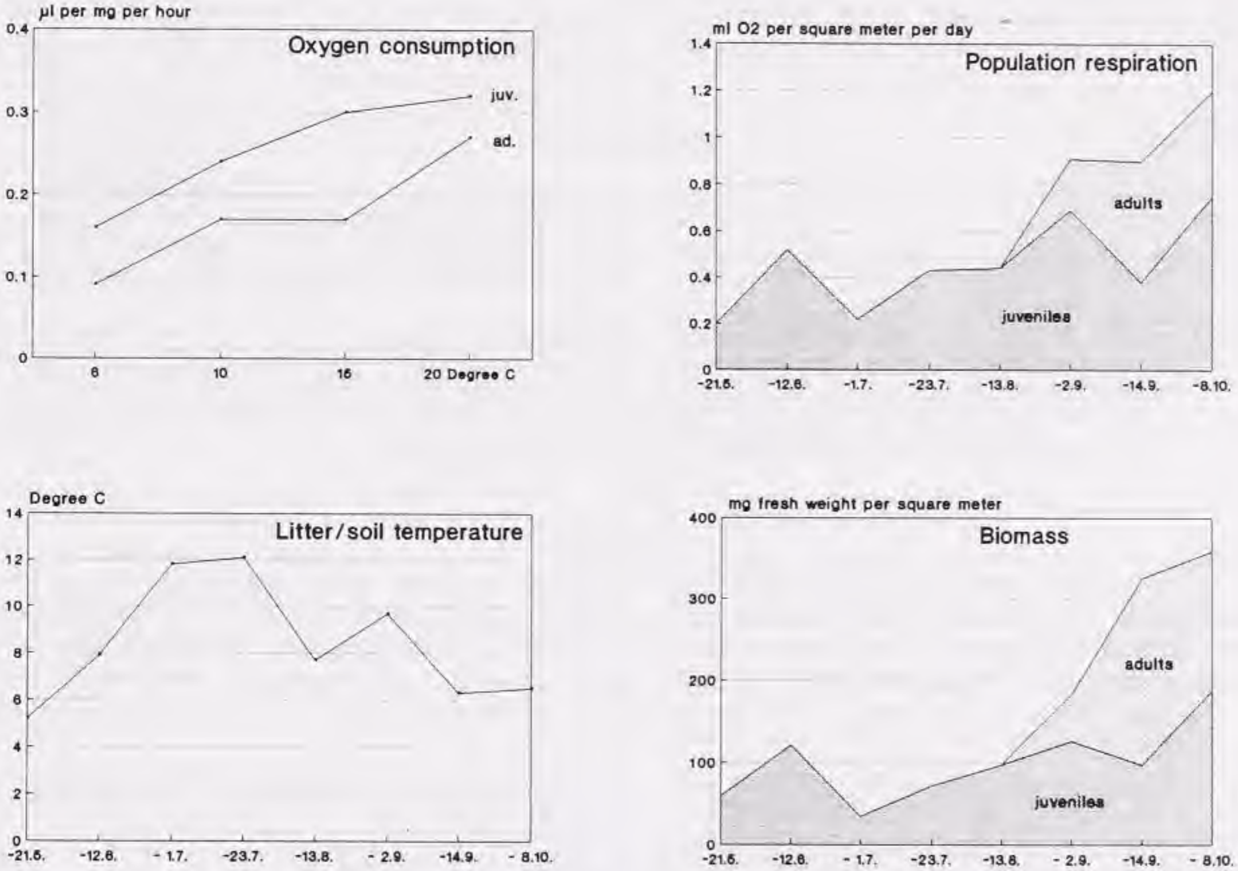


FIG. 4. — Top left: The relationship between oxygen consumption and temperature for juveniles and adults of *O. caroli*. The size range of the two groups are given in Table 3. Bottom left: Mean monthly temperature in the litter layer of the *Alnetum viridis* at 2000 m a.s.l. Bottom right: Mean monthly biomass of juveniles (stage II-VIII) and adults (stage IX) of *O. caroli* in the *Alnetum viridis* (taken from MEYER, 1979). Top right: Oxygen consumption by the whole population over the period May-October.

Source : MNHN, Paris

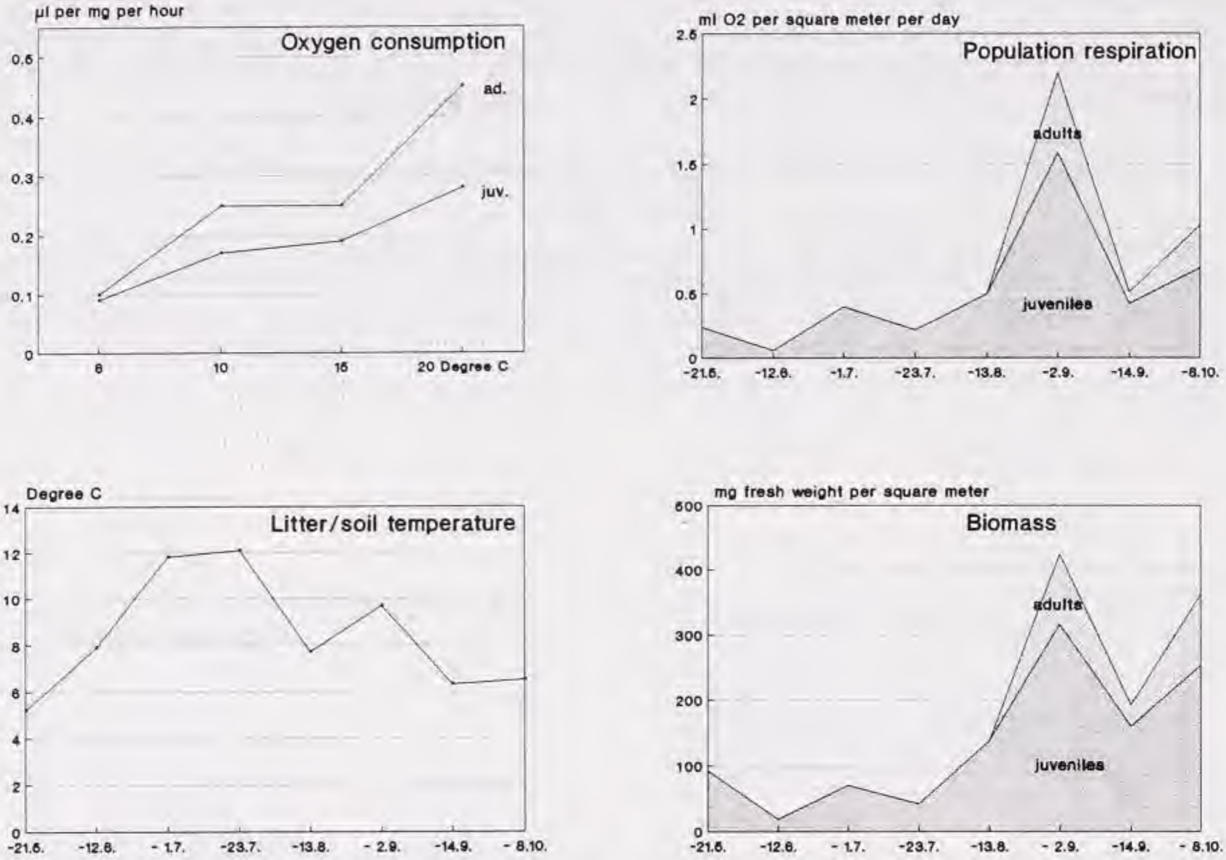


FIG. 5. — Top left: The relationship between oxygen consumption and temperature for juveniles and adults of *H. fonticulorum*. The size ranges of the two groups are given in Table 4. Bottom left: Mean monthly temperature in the litter layer of the *Alnetum viridis* at 2000 m a.s.l. Bottom right: Mean monthly biomass of juveniles (stage II-VIII) and adults (stage IX) of *H. fonticulorum* in the *Alnetum viridis* (taken from MEYER 1979). Top right: Oxygen consumption by the whole population over the period May-October.

DISCUSSION

The results presented above show that in all species there is a relationship between the respiratory rate and size of individual with b-values ranging from 0.2 to 0.92 depending on species and experimental temperature. Only in *H. fonticulorum* does the exponent exceed the known range (0.1 - 1.2, as summarised by PENTEADO *et al.*, 1991) reaching values of 1.41-1.67. The measurements coincided with the usual high autumnal activity of this species in its habitat.

The effects of temperature on millipede metabolism have been studied in several species by GROMYSZ-KALKOWSKA & STOJALOWSKA (1966) and GROMYSZ-KALKOWSKA (1970, 1973, 1974). As in many other invertebrates (WIESER, 1973) there is no continuous increase in oxygen consumption with increasing temperature. "Balanced" respiratory metabolism was found within different temperature ranges depending on the species. Such temperature-insensitive phases frequently occur around the mean temperature to be expected in the environment where the species is active. Such a phenomenon could also be demonstrated during the present study. The oak wood species *E. nanus* shows its "temperature-insensitive" phase between 15°C and 20°C with a Q_{10} of 1.21. This reaction is not fully explained by the temperature conditions in its

Source : MNHN, Paris

habitat, as the daily maxima certainly exceed 15°C for approximately 60 days between June and August, but in no month does the mean temperature reach 15°C (Fig. 3). In the lower temperature range between 10°C and 15°C the Q_{10} is 3.08. This great sensitivity to temperature changes allows the animal to speed up its metabolism as much as possible following hibernation or coldness. Consistently the three subalpine species (*L. saltuvagus, O. caroli* and *H. fonticulorum*) have their greatest sensitivity to temperature changes between 6°C and 10°C with Q_{10} values of 7.9, 3.2 and 7.2. In their habitat at the timberline wet weather is often accompanied by coldness and snowfall even in the summer. Large and rapid temperature changes often occur during the vegetation period. Between June and September the oscillations of the daily mean temperatures in the litter layer of *Alnus viridis* are mostly between 5°C and 10°C (MEYER, 1990). A high sensitivity in this temperature range must be ecologically significant and allows the millipedes to exploit warmer periods efficiently in the overall short growth period. The temperature-insensitive phase of these species occurs between 10°C and 15°C with Q_{10} values of 1.1, 1.5 and 1.2.

Figures 2-5 allow the comparison of the relative influences of the factors temperature, age structure and biomass affecting the final estimates of the population metabolism. In all species the seasonal changes in oxygen consumption of the population reflects changes in population structure and biomass much more than changes in temperature. Similar observations by HASSALL (1983) during investigations into the population metabolism of the isopod *Philoscia muscorum* led to the suggestion that the accuracy with which the population structure and biomass can be assessed is likely to be the most important single factor in determining the metabolism for field populations.

REFERENCES

DWARAKANATH, S. K., 1971. — The influence of body size and temperature upon the oxygen consumption in the millipede *Spirostreptus astenes* (Pocock). *Comp. Biochem. Physiol.*, **38A** : 351-358.

FISCHER, E., 1985. — Sauerstoffverbrauch von 3 subalpinen Diplopodenarten in Abhängigkeit von Temperatur und Körpergewicht. Magisterarbeit, Univ. Innsbruck, 52 pp.

GROMYSZ-KALKOWSKA, K., 1970. — The influence of body weight, external temperature, season of the year, and fasting on respiratory metabolism in *Polydesmus complanatus* L. (Diplopoda). *Folia Biol. (Krakow)*, **18** : 311-326.

GROMYSZ-KALKOWSKA, K., 1973. — Some exogenous and endogenous effects on rate of respiration in *Strongylosoma pallipes* (OLIVIER) (Diplopoda) and behaviour in temperature gradient. *Folia Biol. (Krakow)*, **21** : 251-269.

GROMYSZ-KALKOWSKA, K., 1974. — The effect of some exogenous factors and body weight on oxygen consumption in *Glomeris connexa* C. L. Koch (Diplopoda). *Folia Biol. (Krakow)*, **22** : 37-49.

GROMYSZ-KALKOWSKA, K. & STOJALOWSKA, W., 1966. — Respiratory metabolism in *Orthomorpha gracilis* C. L. Koch (Diplopoda) as a function of temperature and body size. *Folia Biol. (Krakow)*, **14** : 379-389.

HASSALL, M., 1983. — Population metabolism of the terrestrial isopod *Philoscia muscorum* in a dune grassland ecosystem. *Oikos*, **41** : 17-26.

KOFLER, E. & MEYER, E., 1992. — Lebenszyklus, Abundanz und Produktion von *Enantiulus nanus* (LATZEL) in einem inneralpinen Eichenmischwald (Tirol, Österreich). *Ber. nat.- med. Verein Innsbruck*, **Suppl. 10** : 153-166.

MARSONER, P., 1992. — Atmungsstoffwechsel von *Enantiulus nanus* (Diplopoda, Julida). Magisterarbeit, Univ. Innsbruck, 54 pp.

MEYER, E., 1979. — Life-cycles and ecology of High Alpine Nematophora. *In* : M. CAMATINI, *Myriapod Biology*. London, Academic Press : 295-306.

MEYER, E., 1985. — Distribution, activity, life-history and standing crop of Julidae (Diplopoda, Myriapoda) in the Central High Alps (Tyrol, Austria). *Holarctic Ecology*, **8** : 141-150.

MEYER, E., 1990. — Altitude-related changes of life histories of Chordeumatida in the Central Alps (Tyrol, Austria). *In* : A. MINELLI, *Proc. 7th Int. Congr. Myriapodology*. Leiden, Brill : 311-322.

PENTEADO, C. H. S., HEBLING-BERALDO M. J. A. & MENDES E. G., 1991. — Oxygen consumption related to size and sex in the tropical millipede *Pseudonannolene tricolor* (Diplopoda, Spirostreptida). *Comp. Biochem. Physiol.*, **98A** : 265-269.

PENTEADO, C. H. S. & HEBLING-BERALDO, M. J. A., 1991. — Respiratory responses in a Brazilian millipede, *Pseudonannolene tricolor*, to declining oxygen pressure. *Physiol. Zool.*, **64** : 232-241.

Source : MNHN, Paris

PHILLIPSON, J., 1970. — The "best estimate" of respiratory metabolism: its applicability to field situations. *Pol. Arch. Hydrobiol.*, **17** : 31-41.

WIESER, W., 1973. — Temperature relations of ectotherms: a speculative review. *In* : W. WIESER, *Effects of temperature on ectothermic organisms*. Berlin-New York, Springer-Verlag : 1-23.

WOOTEN, R. C. & CRAWFORD, C. S., 1974. — Respiratory metabolism of the desert millipede *Orthoporus ornatus* (GIRARD) (Diplopoda). *Oecologia (Berl.)*, **17** : 179-186.

Source : MNHN, Paris

Variation de la teneur en eau en fonction de la taille corporelle dans une population du diplopode *Polyzonium germanicum*

Guy VANNIER & Jean-François DAVID

CNRS, Laboratoire d'Ecologie Générale, Muséum National d'Histoire Naturelle
4 avenue du Petit Château, F-91800 Brunoy, France

RÉSUMÉ

Des échantillons saisonniers de *Polyzonium germanicum*, comprenant des individus de différente taille, ont été prélevés en forêt d'Orléans. La teneur en eau, exprimée en pourcentage de la masse sèche, a été mesurée chez chaque individu. Quand la masse sèche est prise comme critère de taille, la variation de la teneur en eau en fonction de la taille peut être analysée à l'aide d'un modèle de régression. La relation masse fraîche-masse sèche est linéaire ($Y = a + bX$) et le signe de l'ordonnée à l'origine (a) permet de prévoir le sens de variation de la teneur en eau en fonction de la masse sèche — qui suit une relation hyperbolique si $a \neq 0$. Dans la population étudiée, a est positif, ce qui implique que la teneur en eau décroît quand la masse sèche augmente. Les influences de la saison et du sexe sont analysées de la même façon. Quand le nombre d'anneaux du corps est pris comme critère de taille, cela permet de préciser le stade de développement des individus. Mais l'utilisation des modèles de régresssion se complique et il faut recourir aux comparaisons de moyennes pour étudier les variations de la teneur en eau en fonction de la taille, de la saison et du sexe. Les deux méthodes montrent que la baisse de la teneur en eau quand la taille corporelle augmente est plus marquée chez les femelles que chez les mâles. De plus, quels que soient la taille et le sexe des individus, leur teneur en eau varie saisonnièrement, avec des valeurs plus élevées l'été que l'hiver. Ces résultats sont discutés à la lumière des connaissances sur l'écologie et la biologie de l'espèce.

ABSTRACT

Water content in relation to body size in a population of the millipede *Polyzonium germanicum*.

Polyzonium germanicum individuals of nearly all sizes were collected seasonnaly in the forest of Orléans (France). Water content, expressed as a percentage of dry mass, was determined for each specimen. When body size is equated with dry mass, the changes in water content with body size can be analysed using regression models. The relationship between fresh mass and dry mass is linear ($Y = a + bX$), and the sign of the intercept (a) makes it possible to predict the direction of variation in water content *vs.* dry mass — which is a hyperbolic relation if $a \neq 0$. In the population studied a is positive, *i.e.* water content decreases as dry mass increases. The influence of season and sex is studied in the same way. Body size can also be expressed as a number of rings, which makes it possible to distinguish the stages of development. However, regression analyses are not so straightforward as above, because of curvilinear relationships between mass components and number of body rings. In this case, classic comparisons of means are used to study the changes in water content with body size, sex and season. Both methods show that the decrease in water content as body size increases is more pronounced in females than in males. A seasonal effect on water content is apparent, animals of all stages being more hydrated in warm and dry season than in cold and moist season. These results are discussed taking biological and ecological features of the species into consideration.

VANNIER, G. & DAVID, J.-F., 1996. — Variation de la teneur en eau en fonction de la taille corporelle dans une population du diplopode *Polyzonium germanicum*. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 461-471. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

INTRODUCTION

L'économie hydrique des Diplopodes a surtout été étudiée sous l'angle de la résistance à la dessiccation et des mesures de transpiration, dans le but d'établir des relations entre la distribution géographique des espèces et les conditions climatiques de leur habitat (PERTTUNEN, 1953 ; BARLOW, 1957 ; HAACKER, 1968 ; O'NEILL, 1969 ; CRAWFORD, 1972 ; STEWART & WOODRING, 1973 ; BAKER, 1980 ; WEGENSTEINER, 1982 ; MEYER & EISENBEIS, 1985). D'autres auteurs ont abordé le sujet à travers l'étude de l'ovogénèse (CRAWFORD & WARBURG, 1982) ou l'analyse du milieu intérieur en évaluant les réponses osmotiques des individus selon leur degré de déshydratation et de réhydratation (*e.g.* WOODRING, 1974 ; RIDDLE *et al.*, 1976 ; RIDDLE, 1985).

Nous avons abordé l'étude de la teneur en eau corporelle chez le diplopode *Polyzonium germanicum* Brandt, 1831, dont nous connaissons le cycle biologique (DAVID & COURET, 1985) et les préférences écologiques (DAVID, 1990). Notre contribution diffère des précédentes en ce qu'elle utilise des relations statistiques nouvelles qui mettent en évidence la variation de paramètres caractérisant l'état hydrique des individus à l'intérieur d'un échantillon représentatif de tous les stades de développement au sein d'une population. C'est ainsi que la relation du premier degré qui lie la masse fraîche à la masse sèche permet de connaître le sens de variation de l'hyperbole qui lie la teneur en eau corporelle à la masse sèche considérée comme critère de taille (VANNIER, 1975). Ces variations ont été étudiées en fonction des saisons et en fonction du sexe. D'autres relations ont été formulées en prenant plus classiquement comme critère de taille le nombre d'anneaux pédifères ; elles ont également permis de montrer un effet saisonnier des variations hydriques corporelles.

MATÉRIEL ET MÉTHODES

Quelques dizaines d'individus de *P. germanicum* ont été récoltés environ tous les deux mois au cours d'une période allant de mars 1991 à octobre 1992. Le site de prélèvements est une litière de pins sylvestres (*Pinus silvestris*) dans le massif d'Ingrannes de la Forêt d'Orléans (120 km au sud de Paris) ; le site a été décrit en détail par DAVID (1990) (site n° 10).

L'échantillonnage des animaux a été effectué par une recherche manuelle directe à l'aide de pinces brucelles de manière à capturer l'éventail le plus complet possible des classes de taille présentes dans la litière. Les individus ainsi capturés ont été ramenés sans tarder au laboratoire. Ils ont été pesés à l'aide d'une microélectrobalance (précision 1 microgramme) pour mesurer leur masse fraîche ; placés ensuite dans une étuve (60°C) pendant 48 heures, puis transférés dans un dessiccateur (0% H.R.) pour une durée de 15 jours et obtenir leur masse sèche.

Le nombre d'anneaux pédifères et le sexe ont été déterminés sur les carcasses sèches après un court passage dans une solution de potasse à 10%.

Au cours de notre étude, nous avons traité un ensemble de 279 individus segmentés et 5 oeufs.

RÉSULTATS

Variation de la teneur en eau corporelle par rapport à la masse sèche

1.- Rappel du principe de l'analyse mathématique

La masse fraîche (Y) est lié à la masse sèche (X) par une relation linéaire :

$$Y = a + bX \quad (1)$$

La pente (b) de la droite est toujours positive.

A l'aide de cette équation, on démontre que la relation entre la teneur en eau (W exprimée par rapport à la masse sèche) et la masse sèche (X) est une fonction hyperbolique de la forme :

$$W = a/X + (b-1) \quad (2)$$

Trois cas peuvent se présenter :

- lorsque la constante (a) de l'équation (1) est positive, la dérivée de l'équation (2), $W' = -a/X^2$, est négative ;
- lorsque la constante (a) de l'équation (1) est négative, la dérivée de l'hyperbole est positive ;

Source : MNHN, Paris

- lorsque la constante (a) de l'équation (1) est nulle, l'hyperbole se confond avec une droite parallèle à l'axe des masses sèches et tous les individus ont alors la même teneur en eau :

$W = b - 1.$

Ainsi donc le signe de la constante (a) de la relation linéaire entre la masse fraîche et la masse sèche indique le sens de variation de la teneur en eau corporelle dans la population sans même avoir besoin de la calculer (VANNIER, 1975).

2.- Étude de l'ensemble des individus échantillonnés

La relation qui lie les masses fraîches (Y) aux masses sèches (X) des 279 animaux s'écrit :

$$Y = 0{,}321 + 1{,}979\ X \text{ avec } R^2 = 0{,}97$$

La constante de l'équation est positive à l'intérieur de limites de confiance comprises entre + 0,454 et + 0,188, au seuil de 95% (Fig. 1a).

Dans ce grand échantillon qui comprend la plupart des stades de développement de *P. germanicum*, la moyenne des masses fraîches (± erreur standard) est de 5,039 mg ± 0,264, celle des masses sèches est de 2,384 mg ± 0,131.

La relation qui lie la teneur en eau (W exprimée en pourcentage) à la masse sèche (X exprimée en milligrammes) est donc une hyperbole convexe (Fig. 1b) :

$$W\% = 32{,}1/X + 97{,}9$$

avec une dérivée négative : $W' = -32{,}1/X^2$ et une limite théorique de la teneur en eau corporelle chez les plus grands individus égale à 97,9%. Cet exemple révélant que les jeunes individus sont plus riches en eau que les individus adultes est le plus fréquemment rencontré dans la nature. Les deux autres cas de figure indiquant l'inverse ou montrant des valeurs stables de la teneur en eau quel que soit la masse sèche sont plus exceptionnels. La teneur en eau moyenne des 279 individus est de 121,06% ± 2,05.

3.- Étude des variations saisonnières sans distinction des sexes

La dispersion des points observée sur la Figure. 1b nous a incités à rechercher son origine dans un effet saisonnier. Nous avons analysé nos données en les regroupant en trois catégories correspondant aux animaux récoltés en hiver du 9 décembre au 19 mars (n = 126), ceux récoltés à la fin du printemps et au début de l'été du 21 mai au 9 juillet (n = 104) et ceux récoltés au début de l'automne du 30 septembre au 9 octobre (n = 49).

Les relations linéaires entre masse fraîche (Y) et masse sèche (X) correspondant à ces trois situations s'écrivent comme suit :

- Hiver : $Y_H = 0{,}183 + 1{,}867\ X$ avec $R^2 = 0{,}995$
- Eté : $Y_E = 0{,}173 + 2{,}280\ X$ avec $R^2 = 0{,}987$
- Automne : $Y_A = 0{,}760 + 1{,}843\ X$ avec $R^2 = 0{,}975$

Les constantes (a) de ces trois équations linéaires sont toutes significativement positives au seuil de 95% :

- Hiver : $+ 0{,}264 < a < + 0{,}102$
- Eté : $+ 0{,}326 < a < + 0{,}020$
- Automne : $+ 1{,}037 < a < + 0{,}483$

De cette première analyse, on peut déjà relever que la pente de droite de l'été est significativement plus élevée que celle caractérisant les deux autres saisons ($P < 0{,}001$) ; que la teneur en eau des plus jeunes individus est dans les trois cas de saison supérieure à celle des plus âgés ; celle-ci tend vers des limites significativement différentes : 128% en été, 87 et 84% respectivement en hiver et en automne.

Source : MNHN, Paris

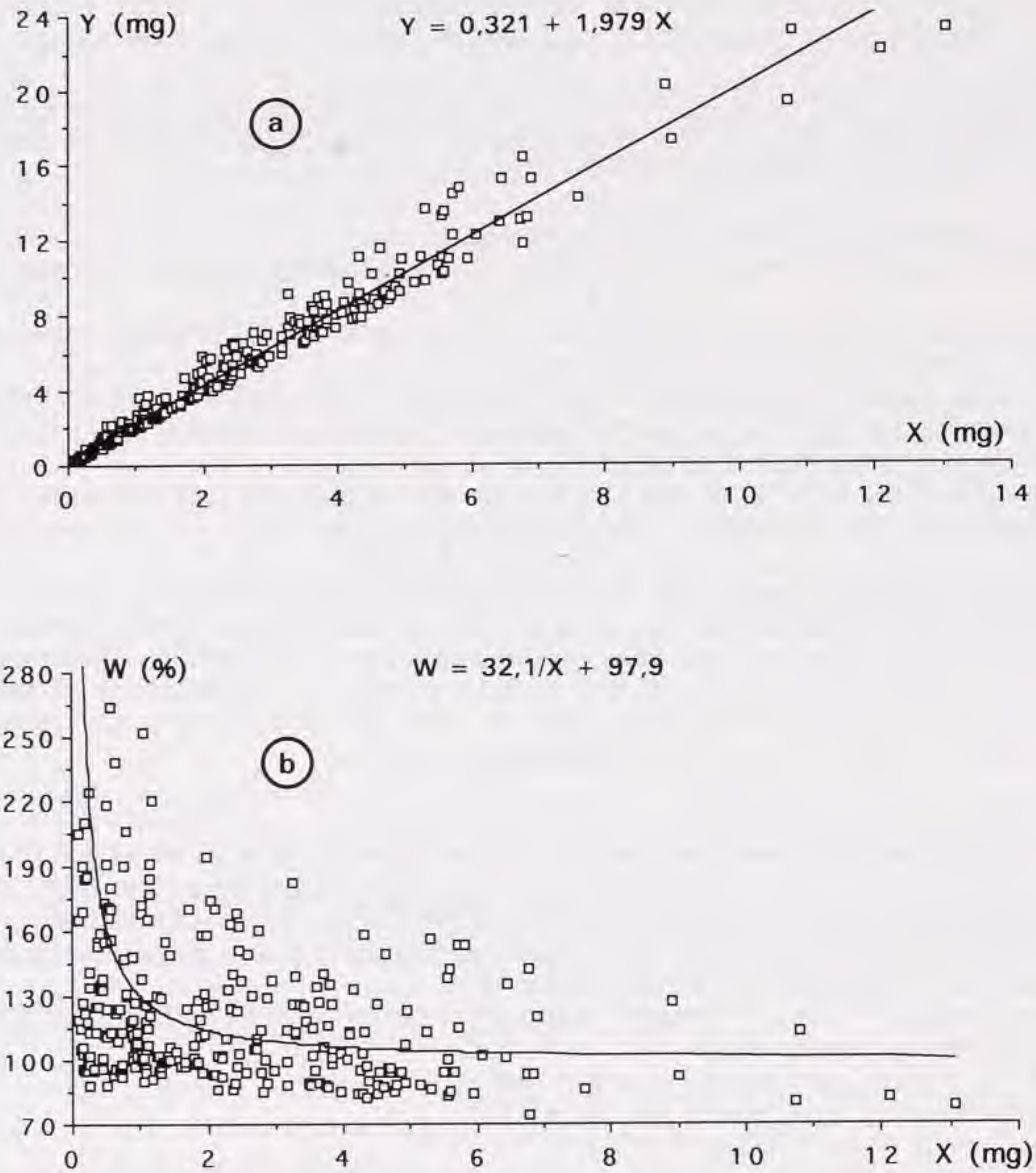


FIG. 1. — Relations hydriques chez les 279 individus échantillonnés de mars 1991 à octobre 1992. **a** : Relation linéaire entre la masse fraîche (Y) et la masse sèche (X). **b** : Relation hyperbolique entre la teneur en eau corporelle (W, en pourcentage de la masse sèche) et la masse sèche (X).

*FIG. 1. — Water relationships for the whole sample (n = 279). **a:** Linear relation between fresh mass (Y) and dry mass (X). **b:** Hyperbolic relation between relative water content (W expressed as a percentage of dry mass) and dry mass (X).*

Les hyperboles correspondant aux trois saisons sont représentées sur la Figure 2. Leur étagement démontre bien que les teneurs en eau des animaux d'été sont systématiquement supérieures à celles des deux autres saisons. On remarque aussi qu'en automne, saison intermédiaire, les individus de petite taille possèdent des teneurs en eau élevées proches de celles mesurées en été ; au contraire les individus de plus grande taille tendent vers des valeurs faibles, proches de celles rencontrées en hiver.

Source : MNHN, Paris

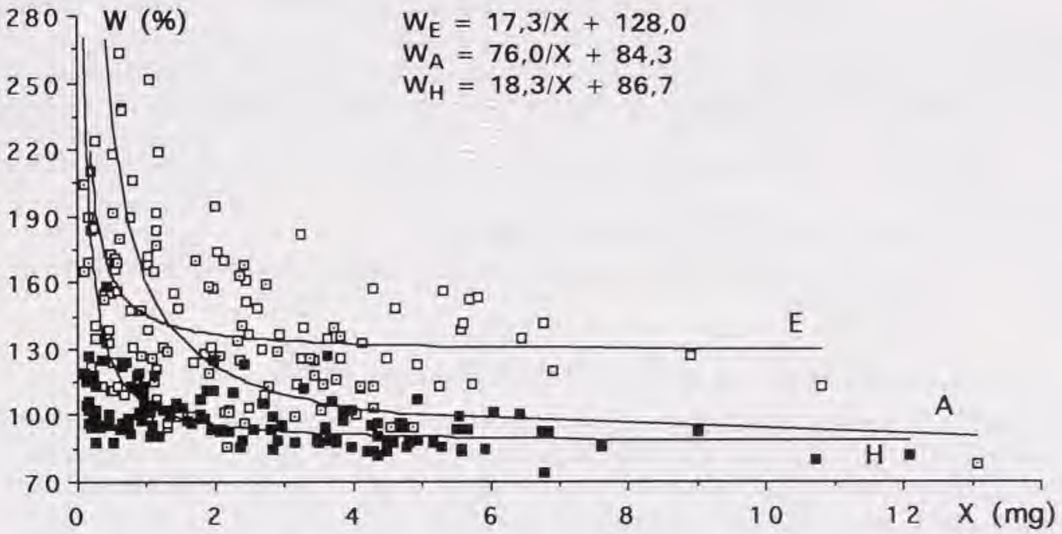


FIG. 2. — Variations saisonnières de la relation hyperbolique entre la teneur en eau corporelle (W, en pourcentage de la masse sèche) et la masse sèche (X) chez les individus récoltés au cours de l'été (E ; carrés blancs), l'automne (A ; carrés pointés) et l'hiver (H ; carrés noirs).

FIG. 2. — Seasonal changes in the hyperbolic relation between water content (W expressed as a percentage of dry mass) and dry mass (X) (E = summer; white squares) (A = autumn; dotted squares) (H = winter; black squares).

4.- Étude des variations saisonnières selon les sexes

a) Les femelles sont analysées avec les jeunes individus indifférenciés en fonction des trois périodes saisonnières : hiver (n = 78), été (n = 64), automne (n = 31). Les équations linéaires entre masses fraîches (Y) et masses sèches (X) correspondant aux trois situations climatiques s'énoncent comme suit :

- Hiver : $Y_H = 0{,}137 + 1{,}867$ X avec $R^2 = 0{,}996$
- Eté : $Y_E = 0{,}203 + 2{,}276$ X avec $R^2 = 0{,}987$
- Automne : $Y_A = 0{,}980 + 1{,}811$ X avec $R^2 = 0{,}974$

Les constantes (a) de ces trois équations linéaires peuvent être considérées comme significativement positives au seuil de 95% en hiver et à l'automne :

- Hiver : + 0,244 < a < + 0,030
- Eté : + 0,411 < a < - 0,005
- Automne : + 1,395 < a < + 0,565

b) De la même manière, les mâles et les jeunes individus indifférenciés ont été rassemblés dans chacune des trois périodes du cycle annuel que nous avons analysées : hiver (n = 69), été (n = 45), automne (n = 22). Les équations linéaires entre masse fraîche (Y) et masse sèche (X) correspondant aux trois saisons s'écrivent comme suit :

- Hiver : $Y_H = 0{,}048 + 1{,}968$ X avec $R^2 = 0{,}990$
- Eté : $Y_E = 0{,}124 + 2{,}286$ X avec $R^2 = 0{,}985$
- Automne : $Y_A = 0{,}288 + 1{,}960$ X avec $R^2 = 0{,}987$

Les constantes (a) des équations linéaires ci-dessus sont comprises dans un intervalle de valeurs significativement positives à l'automne, mais non significativement différentes de zéro l'hiver et l'été :

- Hiver : + 0,134 < a < - 0,038
- Eté : + 0,324 < a < - 0,076
- Automne : + 0,490 < a < + 0,086

La variation de la teneur en eau en fonction de la taille est donc soit décroissante (a > 0), soit à peu près constante (a # 0), mais jamais croissante chez *P. germanicum*. La diminution de

Source : MNHN, Paris

la teneur en eau quand la taille augmente semble aussi plus significative chez les femelles que chez les mâles.

Les équations linéaires montrent en outre que les limites minimales théoriques de la teneur en eau sont variables selon les saisons. En hiver, cette limite est atteinte chez les femelles vers 86,7% et chez les mâles vers 96,8%. En été, elle est atteinte chez les femelles et les mâles vers des valeurs plus élevées et très proches l'une de l'autre, respectivement 127,6% et 128,6%. En automne, les limites ne sont pas significativement différentes de celles calculées en hiver ; elles sont de 81,1% chez les femelles et 96% chez les mâles.

Il ressort nettement de cette analyse que les femelles comme les mâles sont plus riches en eau pendant la période estivale.

Variation de la teneur en eau par rapport au nombre d'anneaux pédifères

1.- Comparaison des valeurs moyennes de la teneur en eau en fonction du sexe et des saisons

Le Tableau 1 répartit l'ensemble de l'échantillon de 279 individus en classes de nombre d'anneaux pédifères, correspondant, pour chaque sexe, à des étapes du développement post-embryonnaire, avec une référence concernant quelques oeufs pondus au début de l'été. Les teneurs en eau moyennes de six classes de tailles biologiquement significatives ont été calculées pour comparer deux saisons opposées.

TABLEAU 1. — Valeurs moyennes de la teneur en eau corporelle (en % de la masse sèche) en fonction du sexe et des saisons au cours du cycle vital de *P. germanicum*.

TABLE 1. — Average water content of P. germanicum *(expressed as a % of dry mass ± standard error), in relation to number of rings, sex and season (Hiver = winter; Eté = summer).*

ANNEAUX PEDIFERES	SEXES	PHASES	STADES	TENEURS EN EAU (% ± E.S.)	
				HIVER	ÉTÉ
0	—	Oeufs	—	—	205 ± 5
8 à 11	—	Immatures	III	103 ± 2	117 ± 15
13 à 15	Mâles	Immatures	IV	—	128 ± 6
"	Femelles	Immatures	IV	—	158 ± 17
17 à 25	Mâles	Adultes	V à VII	102 ± 3	149 ± 9
"	Femelles	Immatures	V à VI	108 ± 6	120 ± 8
28 à 34	Mâles	Adultes	VII à IX	98 ± 2	159 ± 30
"	Femelles	Adultes	VII à IX	91 ± 2	172 ± 16
35 à 40	Mâles	Adultes	VIII à XI	103 ± 4	130 ± 8
"	Femelles	Adultes	VIII à XI	93 ± 2	141 ± 4
41 à 54	Mâles	Adultes	IX à XIII	103 ± 12	136 ± 6
"	Femelles	Adultes	IX à XIII	81 ± 1	131 ± 9

a) En hiver, le pourcentage d'eau des mâles est à peu près constant quel que soit le stade de développement. Il n'est pas significativement différent de celui des immatures du stade III (8-11 anneaux). Chez les femelles, la teneur en eau décroît significativement quand la taille augmente et de manière accentuée à partir de la maturité (28-34 anneaux) pendant la formation des oocytes en période hivernale. On remarquera que les femelles immatures (17-25 anneaux) possèdent une teneur en eau moyenne qui ne diffère pas significativement de celle des formes immatures du stade III (8-11 anneaux).

Source : MNHN, Paris

b) En été, les teneurs en eau moyennes sont toujours plus élevées qu'en hiver, même si les tests de comparaison de STUDENT et de MANN-WHITNEY ne sont pas tous probants. On notera que les erreurs standards dans les deux sexes sont plus élevées en été qu'en hiver (dans huit cas sur neuf) ; cette plus grande dispersion des valeurs de la teneur en eau corporelle pendant la saison chaude peut avoir une signification biologique.

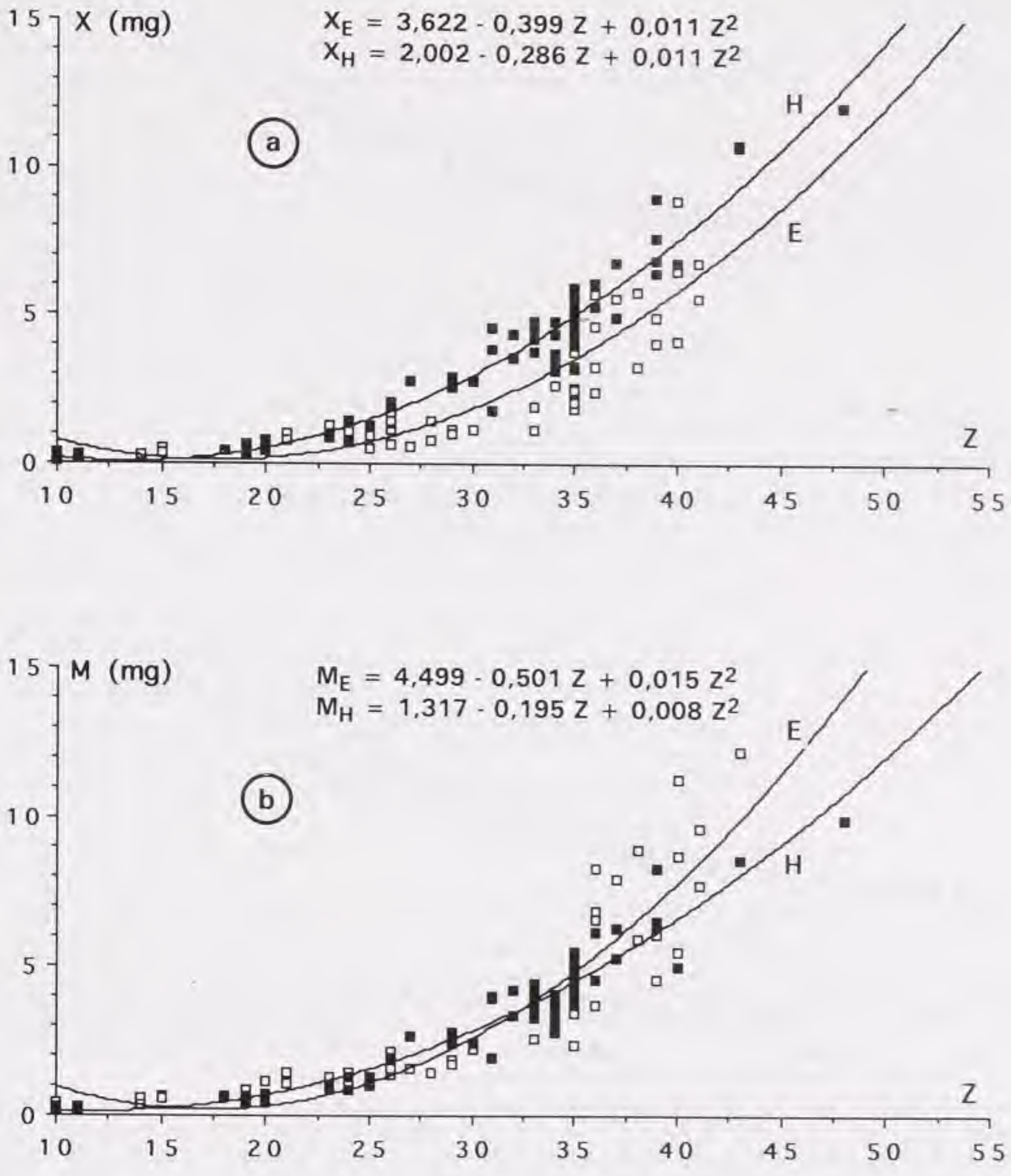


FIG. 3. — Relations entre la masse et le nombre d'anneaux pédifères chez les femelles et les jeunes (*P. germanicum*) récoltés au cours de l'été (E ; carrés blancs) et de l'hiver (H ; carrés noirs). **a** : Variations saisonnières de la relation du second degré entre la masse sèche (X) et le nombre d'anneaux pédifères (Z). **b** : Variations saisonnières de la relation du second degré entre la masse d'eau corporelle (M) et le nombre d'anneaux pédifères (Z).

FIG. 3. — Relationships between mass components and number of podous rings in females and juveniles (P. germanicum) *collected in two seasons (E = summer; white squares) (H = winter; black squares).* ***a:*** *Seasonal changes in the quadratic regression of dry mass (X) versus the number of rings (Z).* ***b:*** *Seasonal changes in the quadratic regression of water mass (M) versus the number of rings (Z).*

Source : MNHN, Paris

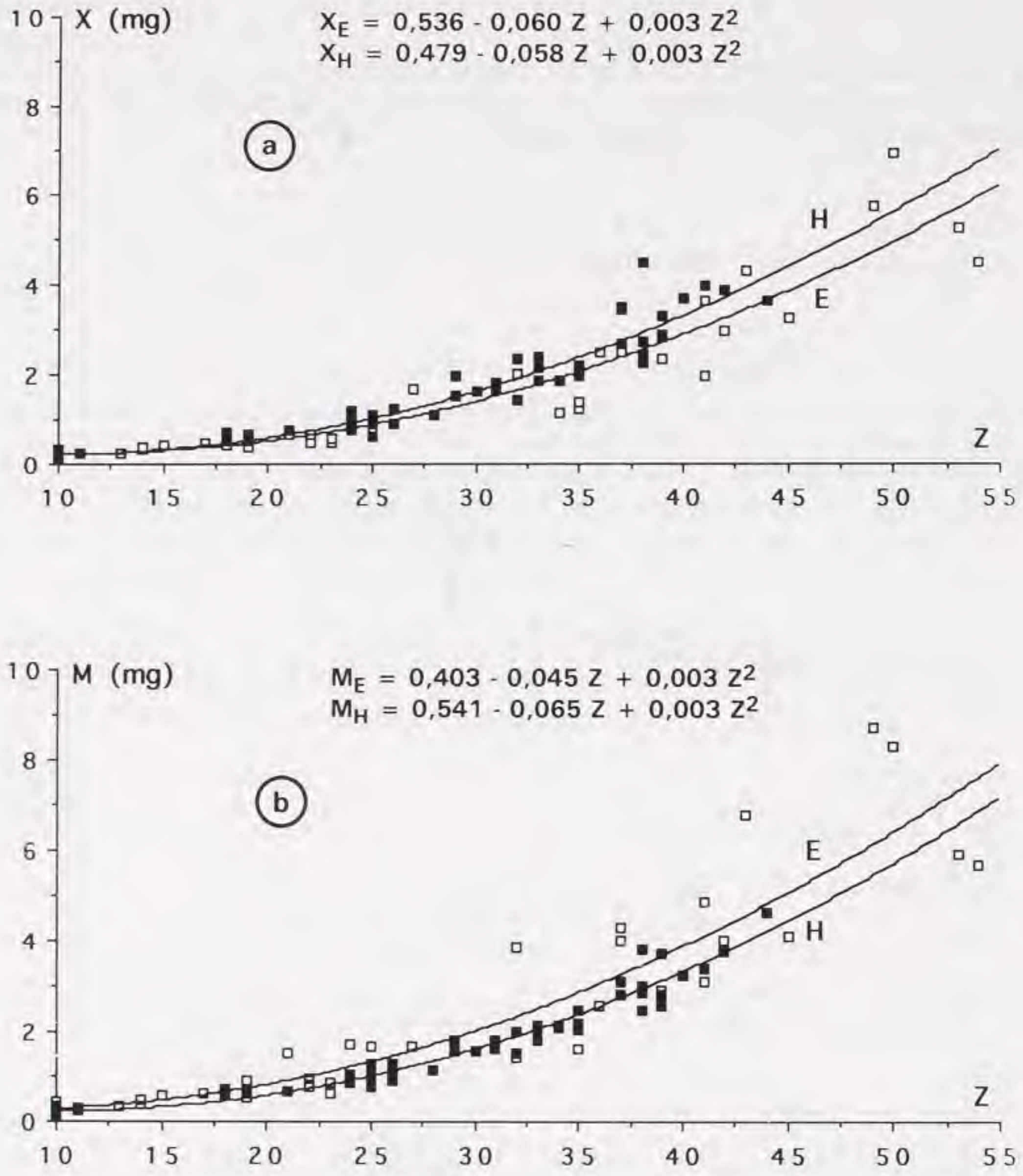


FIG. 4. — Relations entre masse et nombre d'anneaux pédifères chez les mâles et les jeunes (*P. germanicum*) récoltés au cours de l'été (E ; carrés blancs) et de l'hiver (H ; carrés noirs). **a** : Variations saisonnières de la relation du second degré entre la masse sèche (X) et le nombre d'anneaux pédifères (Z). **b** : Variations saisonnières de la relation du second degré entre la masse d'eau corporelle (M) et le nombre d'anneaux pédifères (Z).

FIG. 4. — Relationships between weight components and number of podous rings in males and juveniles (P. germanicum) *collected in two seasons (E = summer; white squares) (H = winter; black squares).* ***a:*** *Seasonal changes in the quadratic regression of dry mass (X) versus the number of rings (Z).* ***b:*** *Seasonal changes in the quadratic regression of water mass (M) versus the number of rings (Z).*

2.- Étude complémentaire des variations saisonnières en fonction du sexe

Du point de vue dimensionnel, le nombre d'anneaux pédifères a l'avantage d'être appréhendé indépendamment des mesures pondérales et permet donc de tester si les variations saisonnières de la teneur en eau sont imputables soit aux changements de masse d'eau, soit aux variations de masse sèche.

Source : MNHN, Paris

Chez les formes indifférenciées correspondant au stade III du développement, la masse sèche est la même dans les échantillons d'hiver et d'été (0,21 mg) ; cependant la masse d'eau est significativement plus élevée en été qu'en hiver (respectivement 0,36 mg et 0,21 mg ; $P < 0{,}01$).

Chez les femelles et chez les mâles on compare les équations de régression soit de la masse sèche (X), soit de la masse d'eau (M) en fonction du nombre d'anneaux pédifères (Z) entre l'hiver et l'été. Le fait nouveau est que toutes les régressions sont des fonctions du second degré.

Chez les jeunes et les femelles, les variations de la masse sèche (X) en fonction du nombre d'anneaux pédifères (Z) correspondent aux trinômes suivants (Fig. 3a) :

- Hiver : $Y_H = 2{,}002 - 0{,}286\ Z + 0{,}011\ Z^2$ avec $R^2 = 0{,}950$
- Eté : $Y_E = 3{,}622 - 0{,}399\ Z + 0{,}011\ Z^2$ avec $R^2 = 0{,}806$

A nombre d'anneaux pédifères égal, la masse sèche tend à être plus faible en été qu'en hiver, principalement chez les femelles adultes à partir du stade VII porteur de 28 anneaux et plus.

L'évolution de la masse d'eau (M) chez les femelles par rapport au même critère de taille (Z) suit le même type d'équation (Fig. 3b) :

- Hiver : $M_H = 1{,}317 - 0{,}195\ Z + 0{,}008\ Z^2$ avec $R^2 = 0{,}944$
- Eté : $M_E = 4{,}499 - 0{,}501\ Z + 0{,}015\ Z^2$ avec $R^2 = 0{,}844$

La masse d'eau corporelle tend à être plus élevée en été qu'en hiver. Cependant, un chevauchement des deux courbes vers le 35ème anneau montre que les femelles de tailles comprises entre 28 et 34 anneaux (stades VII à IX) ont une masse d'eau plus faible en été qu'en hiver ; chez les femelles plus grandes ou plus petites la tendance générale est respectée.

Chez les jeunes et les mâles, les équations du second degré liant la masse sèche (X) au nombre d'anneaux pédifères (Z) s'écrivent comme suit (Fig. 4a) :

- Hiver : $X_H = 0{,}479 - 0{,}058\ Z + 0{,}003\ Z^2$ avec $R^2 = 0{,}927$
- Eté : $X_E = 0{,}536 - 0{,}060\ Z + 0{,}003\ Z^2$ avec $R^2 = 0{,}887$

A nombre d'anneaux pédifères égal, la masse sèche est plus faible chez les individus de l'été, mais de manière moins marquée que chez les femelles.

Les variations de la masse d'eau (M) chez les mâles en fonction du nombre d'anneaux pédifères (Z) sont aussi représentées sur la Figure 4b et les équations s'écrivent :

- Hiver : $M_H = 0{,}541 - 0{,}065\ Z + 0{,}003\ Z^2$ avec $R^2 = 0{,}965$
- Eté : $M_E = 0{,}403 - 0{,}045\ Z + 0{,}003\ Z^2$ avec $R^2 = 0{,}844$

La masse d'eau corporelle tend à être plus élevée en été qu'en hiver, mais de façon moins accentuée que chez les femelles.

Dans les deux sexes, on a constaté les mêmes tendances : à niveau de développement égal, les masses sèches sont plus élevées en hiver qu'en été, alors que c'est l'inverse pour les masses d'eau. Ces deux observations ont pour conséquence de réduire la valeur relative de la teneur en eau en hiver et de l'augmenter en été. Ce phénomène dépendant des stades a moins d'amplitude chez les mâles que chez les femelles.

DISCUSSION & CONCLUSION

Notre étude sur *P. germanicum* reprend des points traités par les auteurs qui ont abordé le problème de l'économie hydrique chez les diplopodes. De manière non équivoque, nous savons maintenant que les teneurs en eau corporelle varient selon les saisons et sont dépendantes de l'âge et du sexe des individus selon des fonctions spécifiques (hyperboles, trinômes). Cependant, il n'est pas très aisé de reconnaître l'influence prépondérante d'un facteur ou d'un autre sur les variations de la teneur en eau corporelle dans une population aussi complexe que celle de *P. germanicum* dont le cycle biologique se développe sur plusieurs années (DAVID & COURET, 1985).

Source : MNHN, Paris

Parmi les facteurs intrinsèques qui influent sur les variations de la teneur en eau des individus, la croissance est déterminante. Dans nos relevés, nous avons montré que la teneur en eau tend à diminuer quand la taille augmente. Cette diminution est surtout visible en hiver, quand la dispersion des mesures hydriques est la plus étroite. En outre, la comparaison entre sexes montre que cette décroissance concerne principalement les femelles. Deux interprétations peuvent être avancées :

1. La masse sèche des femelles à stade égal est plus élevée que celle des mâles, ce qui peut se répercuter sur le calcul de la valeur relative de la teneur en eau.

2. Les tissus reproducteurs (corps gras, ovocytes) peuvent peser sur cette différence entre sexes, car on constate que la teneur en eau diminue surtout chez les femelles adultes reproductrices (Tableau 1).

BAKER (1980) a également mis en évidence une diminution de la teneur en eau en fonction de la masse sèche chez le iulide *Ommatoiulus moreleti* dont les femelles sont plus riches en eau que les mâles, contrairement à *P. germanicum*.

Les saisons marquent de leur empreinte les variations de la teneur en eau corporelle. L'opposition été-hiver, saison chaude-saison froide, est manifeste (Figs. 2-4, Tableau 1). Plusieurs mécanismes liés à la phénologie du cycle vital de *P. germanicum* peuvent être mis en cause :

- La masse sèche d'un individu de stade donné tend à être plus faible en été qu'en hiver. A cela trois explications possibles : a) Le rejet de la mue en période estivale ; mais dans nos relevés du début de l'été beaucoup d'individus n'avaient pas encore mué. b) Sachant que chez *P. germanicum* le stock d'ovocytes se constitue en hiver et que la ponte a lieu à la fin du printemps (COURET & DAVID, 1985 ; DAVID & COURET, 1985), le corps des femelles se trouve donc allégé au début de l'été. c) Chez les deux sexes, les masses de graisses ont aussi leur part d'influence sur les fluctuations de la masse sèche. Nous développerons cet aspect dans un prochain article.

- La masse d'eau d'un individu à un stade donné tend à être plus élevée en été qu'en hiver. Nous proposons l'interprétation suivante : au début de l'été, avant la période d'exuviation, les animaux augmenteraient leurs réserves hydriques, comme l'un de nous l'a observé chez quatre espèces de Collemboles (VANNIER, 1981). Nous avons effectivement observé que de nombreux individus possédant des teneurs en eau élevées étaient proches de l'ecdysis. Les animaux du stade IV sont particulièrement représentatifs de ce phénomène de reprise hydrique. On ne les rencontre qu'au début de l'été et le plus souvent, ils viennent de muer. Leur teneur en eau (Tableau 1) est beaucoup plus élevée (128% chez les mâles, 158% chez les femelles) que celle des stades III d'hiver qui les ont précédés (103%).

Des variations saisonnières de la teneur en eau corporelle ont été signalées chez plusieurs espèces de diplopodes dans la littérature. Des valeurs maximales ont été trouvées au printemps et en été chez *Ommatoiulus moreleti* par BAKER (1980), comme chez *P. germanicum* de la forêt d'Orléans. Selon cet auteur, cela pourrait s'expliquer par des modifications de structure dans la population, comme la présence de gros individus à faible teneur en eau dans les échantillons d'hiver. Cette explication ne convient pas pour *P. germanicum* dans notre étude. Chez les Spirostreptidae, *Archispirostreptus tumuliporus* et *Orthoporus ornatus*, le maximum hydrique est atteint en hiver pour la première espèce qui vit en Israël et en été pour la seconde vivant dans le Sud des Etats-Unis. Ces observations ont été rapportées par CRAWFORD *et al.* (1987) et coïncident avec la saison humide. Selon ces auteurs, l'accroissement du taux hydrique corporel chez ces espèces peuplant des zones arides serait dû à l'ingestion de nourriture humide.

L'analyse que nous faisons de ces données bibliographiques peut se résumer en trois points : a) Le maximum hydrique au printemps et en été coïncide avec la période des mues chez *Ommatoiulus moreleti* (BAKER, 1980). b) C'est également avec les mues et avant la sortie en surface de *Archispirostreptus tumuliporus* que les teneurs en eau les plus fortes sont mesurées (CRAWFORD *et al.*, 1987). c) De même, l'augmentation de la masse d'eau dans la cuticule et les

Source : MNHN, Paris

tissus chez *Orthoporus ornatus* se produit en fin de saison sèche, avant la mue, précédant la période d'activité en saison humide (CRAWFORD, 1978).

Du point de vue biologique, il semble bien que *P. germanicum* réagisse de la même manière, avec une augmentation significative de la teneur en eau corporelle dans les mois qui encadrent la période de mue. L'économie hydrique des diplopodes serait davantage régie par des facteurs intrinsèques (crises physiologiques) que par des facteurs extrinsèques (climat).

RÉFÉRENCES

BAKER, G. H., 1980. — The water and temperature relationships of *Ommatoiulus moreletii* (Diplopoda: Iulidae). *J. Zool. (Lond.)*, **190** : 97-108.

BARLOW, C. A., 1957. — A factorial analysis of distribution in three species of diplopods. *Tijdschr. Entomol.*, **100** : 349-426.

COURET, T. & DAVID, J. F., 1985. — Recherche des stades de maturité sexuelle chez le Diplopode *Polyzonium germanicum* Brandt, 1831 (Polyzoniida). *Rev. Ecol. Biol. Sol*, **22** : 247-258.

CRAWFORD, C. S., 1972. — Water relations in a desert millipede *Orthoporus ornatus* (Girard) (Spirostreptidae). *Comp. Biochem. Physiol.*, **42(A)** : 521-535.

CRAWFORD, C. S., 1978. — Seasonal water balance in *Orthoporus ornatus*, a desert millipede. *Ecology*, **59** : 996-1004.

CRAWFORD, C. S., BERCOVITZ, K. & WARBURG, M. R., 1987. — Regional environments, life-history patterns, and habitat use of Spirostreptid millipedes in arid regions. *Zool. J. Linn. Soc.*, **89** : 63-88.

CRAWFORD, C. S. & WARBURG, M. R., 1982. — Water balance and apparent oocyte resorption in desert millipedes. *J. exp. Zool.*, **222** : 215-226.

DAVID, J.-F., 1990. — Habitat dimensions of Diplopoda in a temperate forest on acid soil. *Rev. Ecol. Biol. Sol*, **27** : 95-112.

DAVID, J. F. & COURET, T., 1985. — Le cycle biologique du Diplopode *Polyzonium germanicum* Brandt, 1831 (Polyzoniida). *Rev. Ecol. Biol. Sol*, **22** : 367-380.

HAACKER, U., 1968. — Deskriptive, experimentelle und vergleichende Untersuchungen zur Autökologie rhein-mainischer Diplopoden. *Oecologia (Berl.)*, **1** : 87-129.

MEYER, E. & EISENBEIS, G., 1985. — Water relations in millipedes from some Alpine habitat types (Central Alps, Tyrol) (Diplopoda). *Bijdr. Dierkd.*, **55** : 131-142.

O'NEILL, R. V., 1969. — Comparative desiccation tolerance in seven species of millipedes. *Am. Midl. Nat.*, **82** : 182-187.

PERTTUNEN, V., 1953. — Reactions of diplopods to the relative humidity of the air. *Ann. Zool. Soc. Zool. -Bot. Fenn. Vanamo*, **16** : 1-69.

RIDDLE, W. A., 1985. — Hemolymph osmoregulation in several Myriapods and Arachnids. *Comp. Biochem. Physiol.*, **80(A)** : 313-323.

RIDDLE, W. A., CRAWFORD, C. S. & ZEITONE, A. M., 1976. — Patterns of hemolymph osmoregulation in three desert arthropods. *J. Comp. Physiol.*, **112(B)** : 295-305.

STEWART, T. C. & WOODRING, J. P., 1973. — Anatomical and physiological studies of water balance in the millipedes *Pachydesmus crassicutis* (Polydesmida) and *Orthoporus texicolens* (Spirobolida). *Comp. Biochem. Physiol.*, **44(A)** : 735-750.

VANNIER, G., 1975. — Les trois cas de figure de la relation teneur en eau corporelle-poids sec chez un insecte Collembole au cours du cycle annuel. *C. R. Acad. Sci. Sér. D*, **280** : 117-120.

VANNIER, G., 1981. — Déséquilibre de la balance hydrique corporelle chez quatre espèces d'insectes Collemboles après un jeûne de courte durée. *Rev. Ecol. Biol. Sol*, **18** : 29-38.

WEGENSTEINER, R., 1982. — Zusammenhänge zwischen der ökologischen Potenz von *Polyzonium germanicum* Brandt (Diplopoda, Colobognatha) und Standortparametern im Vorderen Rotmooz (Lunz, NÖ). *Zool. Jahrb. Syst.*, **109** : 309-327.

WOODRING, J. P., 1974. — Effects of rapid and slow dehydration on the hemolymph osmolarity and Na^+-K^+ concentration in the millipede *Pachydesmus crassicutis*. *Comp. Biochem. Physiol.*, **49(A)** : 115-119.

Source : MNHN, Paris

Source : MNHN, Paris

The Respiratory Response to Changing Temperature in Millipedes belonging to the Genus *Glomeris* Latreille, 1802

Vladimir SUSTR

Institute of Soil Biology, Academy of Sciences of the Czech Republic, 370 05 Ceske Budejovice, Czech Republic

ABSTRACT

The relationship between respiration rate and temperature of 3 millipede species: *Glomeris marginata* (Villers, 1789), *Glomeris hexasticha* Brandt, 1833 and *Glomeris balcanica* (Verhoeff, 1906), with different geographical distribution was measured and analysed. Simple linear relationship was found in *G. marginata*. A zone of the relative independence of respiration rate on temperature in the temperature range 15-20°C was observed in *G. hexasticha*. The zone was less apparent in *G. balcanica*. Specific respiration rates were higher in males than in females in all species. Possible ecological significance of the difference in the respiration-temperature dependence was discussed.

RÉSUMÉ

Réponse respiratoire aux changements de température chez les diplopodes du genre *Glomeris* Latreille, 1802.

Les relations entre le métabolisme respiratoire et la température ont été mesurées et analysées chez trois espèces de diplopodes présentant des aires de répartition différentes : *Glomeris marginata* (Villers, 1789), *Glomeris hexasticha* Brandt, 1833 et *Glomeris balcanica* (Verhoeff, 1906). Une relation linéaire simple a été mise en évidence chez *G. marginata*. Chez *G. hexasticha*, le métabolisme respiratoire est relativement indépendant de la température, entre 15°C et 20°C, phénomène moins évident chez *G. balcanica*. Pour toutes les espèces, les taux respiratoires sont plus élevés chez les mâles que chez les femelles. La possibilité d'une interprétation écologique de cette différence dans la relation respiration-température est discutée.

INTRODUCTION

Glomeris balcanica is a dominant species of the soil macrofauna in extreme biotopes on an altitudinal gradient on Mt. Olympus and in a *Quercus coccifera* formation in Northern Greece. The detailed description of its biology and ecology, including respiration activity, was given by IATROU (1989) and IATROU & STAMOU (1989). *Glomeris marginata* is a common inhabitant of litter layers in deciduous forests of western Europe, *Glomeris hexasticha* is a middle and east European species. The biology and ecology of *G. marginata* and *G. hexasticha* was described by DUNGER & STEINMETZGER (1981). More information about respiration-temperature relationships have been published (e.g. PENTEADO & MENDES, 1981; GROMYSZ-KALKOWSKA & TRACZ, 1983). However, different authors have used different experimental conditions, so

SUSTR, V., 1996. — The respiratory response to changing temperature in millipedes belonging to the genus *Glomeris* Latreille, 1802. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 473-476. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

generalizations are difficult. The main aim of this study was to test differences between the species in specific metabolic rate (SMR) and to assay the SMR - temperature relationship using almost identical experimental procedure and the same method of measurement.

MATERIAL AND METHODS

The specimens of *G. balcanica* were collected in the northwest of Greece, some 20 km from Thessaloniki about 400 m a.s.l. in June 1991 (leg. TAJOVSKY), and, after transport to our laboratory, kept for 3 weeks at 15°C in darkness. A mixture of *Quercus coccifera* and *Quercus robur* litters was used as food. Specimens of *G. marginata* were collected from a *Quercus pubescens* forest in Ruoms near Montélimar (south of France) at an altitude 400 m a.s.l. in May 1991 (leg. FROUZ) and kept on *Q. robur* litter in similar conditions as *G. balcanica*. Individuals of *G. hexasticha* were collected in a mixed oak forest near Netolice in South Bohemia at an altitude from 485 to 570 m a.s.l. in May 1991 (leg. SUSTR & TAJOVSKY), and kept on *Quercus robur* litter for 1- 3 weeks in conditions similar to those for *G. balcanica*. Oxygen consumption was measured in a Warburg respirometer over a 5-hour period; 30 minutes were allowed for thermostabilization. The respiration rate of every animal was measured successively at 5, 10, 15, and 20°C during 4 days of experiment. Animals were reared in the laboratory culture (15°C, dark, with food) for approximately 19 hours between the measurements. Seventeen individuals of *G. hexasticha* (7 males and 10 females), 15 specimens of *G. balcanica* (2 males and 13 females) and 16 individuals of *G. marginata* (7 males and 9 females), with body mass in the range of 0.030 - 0.219 g, 0.091 - 0.282 g, and 0.073 to 0.399 g, respectively, were used in the experiments. Q_{10} values were calculated according to the equation $Q_{10} = (k_1/k_2)^{10/(t1-t2)}$, where k_1 and k_2 are mean respiration rates at temperatures t1 and t2 respectively.

RESULTS

Specific metabolic rate (SMR)-temperature curves are shown in Figure 1. ANOVA indicated a significant effect of temperature on SMR in all three species ($F = 36.6$, $P < 0.01$ in *G. marginata*, $F = 40.4$, $P < 0.01$ in *G. hexasticha* and $F = 49.0$, $P < 0.01$ in *G. balcanica*). The shapes of the curves were similar in both sexes of the same species (see Table 1). An almost linear curve was observed in *G. marginata*. The increase of SMR with increasing temperature was larger from 5 to 15°C than from 15 to 20°C in *G. balcanica*. A small range of relative temperature independence (RRTI) was observed between 15 and 20°C in *G. hexasticha* (Fig. 1, Table 1).

SMR values were higher in males than in females. Differences were significant in *G. hexasticha* ($F = 5.8$, $P < 0.02$) and in *G. balcanica* ($F = 8.5$, $P < 0.01$). In *G. balcanica*, however, the comparison is disputable because of the limited number of males used in the experiment.

The SMR of *G. marginata* was significantly lower than those of *G. balcanica* and *G. hexasticha* at 5 and 15°C ($F = 14.6$, $P < 0.01$ and $F = 11.1$, $P < 0.01$ respectively).

The mean individual body mass was 0.090 g in *G. hexasticha*, 0.175 g in *G. balcanica*, and 0.187 g in *G. marginata*. Changes in body mass were not significant during the experiment ($F < 0.01$, $P > 0.9$) for any species.

TABLE 1. — Q_{10} coefficients in three species of glomerid millipedes in the temperature range from 5°C to 20°C.

Species	Temperature range					
	5-10	5-15	10-15	5-20	10-20	15-20
Glomeris hexasticha	2.0	2.3	2.6	1.9	1.8	1.2
Glomeris hexasticha males	1.9	2.3	2.9	1.8	1.8	1.1
Glomeris hexasticha females	2.3	2.3	2.3	1.9	1.8	1.3
Glomeris balcanica	2.8	3.0	3.1	2.3	2.1	1.3
Glomeris balcanica males	4.4	4.2	4.0	3.0	2.5	1.5
Glomeris balcanica females	2.7	2.7	2.7	2.1	1.9	1.3
Glomeris marginata	4.3	3.0	2.1	2.5	2.0	1.8
Glomeris marginata males	4.0	3.1	2.3	2.5	2.0	1.8
Glomeris marginata females	5.3	3.2	2.0	2.7	1.9	1.9

Source : MNHN, Paris

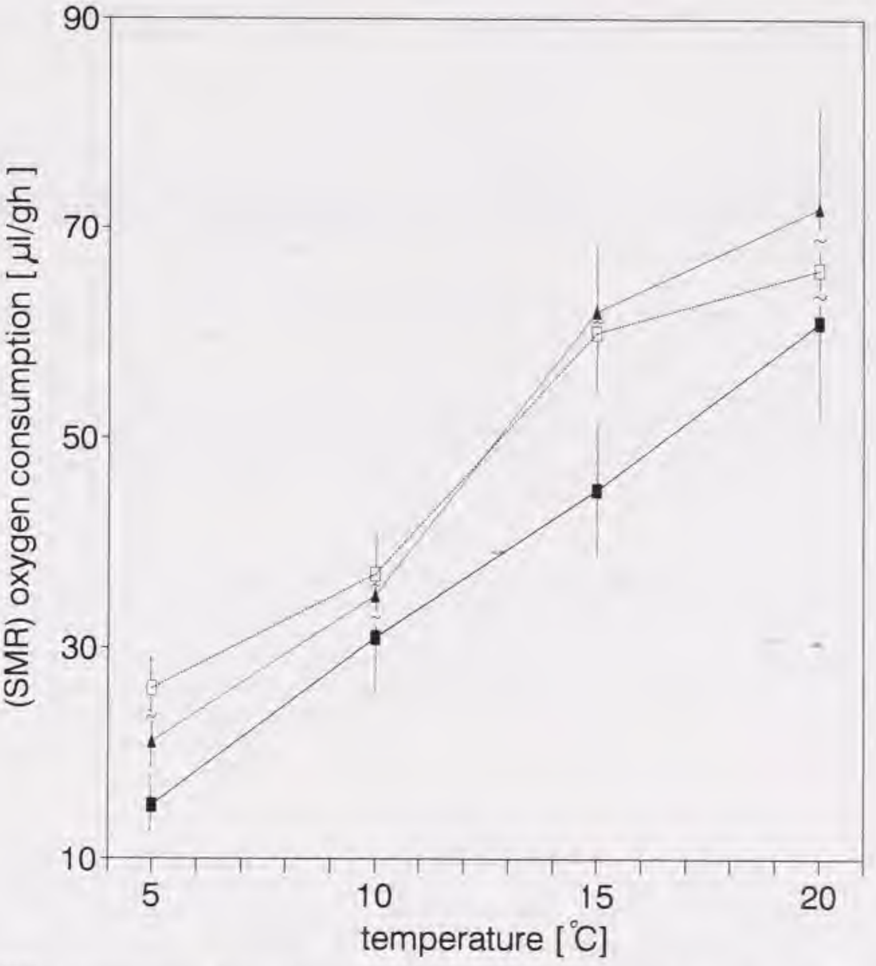


FIG. 1. — Mean SMR - temperature relationships in three species of millipedes. Errors bars: 95% confidence intervals, filled triangle: *Glomeris balcanica*, filled square: *Glomeris marginata*, empty square: *Glomeris hexasticha*.

DISCUSSION

G. marginata, in agreement with its geographical distribution, would be best adapted to an oceanic climate with relatively variable weather. The population used in this study lives in a relatively exposed, warm and dry site. Adaptation to a microclimate with frequent temperature fluctuations, as well as relatively low locomotion activity appears to have prevented *G. marginata* from establishing an RRTI (that does or does not occur in a species). A wide range of preferred temperatures (18°C to 26°C) was observed in *G. marginata* in laboratory by DUNGER & STEINMETZGER (1981). The site of collection of *G. hexasticha* has a forest microclimate without great temperature fluctuations. These conditions may have enabled the establishment of a clearly expressed RRTI between 15°C and 20°C in the species. Its prefered temperature of 20°C was reported in laboratory by DUNGER & STEINMETZGER (1981). The lack of RRTI should be expected in *G. balcanica* because of high temperature fluctuations in the soil organic layer in *Q. coccifera* formation. However, *G. balcanica* shows greater locomotion activity and irritability than *G. marginata* and *G. hexasticha*. The difference between the standard and active metabolic rate may be larger and the RRTI consequently more expressed. The combination of the above mentioned factors contributes to the establishment of the RRTI, which is less apparent in comparison to *G. hexasticha*. The placement of the RRTI (between 15°C and 20°C) corresponds

Source : MNHN, Paris

to a temperature optimum of food consumption (IATROU & STAMOU, 1989) and with Q_{10} values obtained by IATROU (1989).

REFERENCES

DUNGER, W. & STEINMETZGER, K., 1981. — Ökologische Untersuchungen an Diplopoden einer Rasen-Wald-Catena im Thüringer Kalkgebiet. *Zool. Jb. Syst.*, **108** : 519-553.

GROMYSZ-KALKOWSKA, K. & TRACZ, H., 1983. — Effect of temperature, food kind and body weight on the oxygen consumption by *Proteroiulus fuscus* (Am Stein) (Diplopoda, Blaniulidae). *Ann. Warsaw. Agricult. Univ. - SGGW-AR, For. a. Wood Technol.*, **30** : 35-42.

IATROU, G. D., 1989. — Dynamics and activity of the diplopod *Glomeris balcanica* in the soil subsystem of an evergreen-sclerophyllous formation in Mt. Hortiatis. Ph. D. Thesis, Aristotelian University of Thessaloniki (In Greek), 216 pp.

PENTEADO, C. H. S. & MENDES, E; G., 1981. — Respiratory metabolism and tolerance in a tropical millipede, *Rhinocricus padbergi* Verhoeff, 1938. III: the response to temperature variations. *Rev. Brasil. Biol.*, **41** : 499-509.

IATROU, G. D. & STAMOU, G. P., 1989. — Seasonal activity patterns of *Glomeris balcanica* (Diplopoda, Glomeridae) in an evergreen-sclerophyllous formation in northern Greece. *Rev. Ecol. Biol. Sol*, **26** : 491-503.

Source : MNHN, Paris

Submersion Tolerance of some Diplopod Species

***Klaus Peter* ZULKA**

Institute of Zoology, University of Vienna
Althanstr. 14, A-1090 Vienna, Austria

ABSTRACT

Submersion tolerance of *Polydesmus denticulatus* was compared to that of other diplopod species. About ten specimens of five species were placed individually in plastic tubes and flooded in an aquarium with aerated water (temperature 9±1°C). The highest median tolerance times were found in *Polydesmus denticulatus*, but one specimen of *Brachyiulus bagnalli* even reached a higher maximum of 65 days submersion. The other species are considerably less tolerant. In the four julid species median submersion tolerance times are significantly correlated with the surface/volume-ratio. *Polydesmus denticulatus*, however, is an outlier, and shows comparably higher tolerance values. The possible mechanisms of submersion tolerance are discussed.

RÉSUMÉ

Tolérance à l'immersion chez quelques espèces de diplopodes.

La tolérance à l'immersion de *Polydesmus denticulatus* a été comparée à celle d'autres espèces de diplopodes. Une dizaine de spécimens de cinq espèces ont été placés individuellement dans des tubes de matière plastique et immergés dans un aquarium contenant de l'eau aérée (température 9±1°C). En moyenne, la plus longue durée de tolérance à ce milieu est présentée par *Polydesmus denticulatus*. Cependant un invidu de *Brachyiulus bagnalli* a atteint la durée maximale de 65 jours d'immersion. Les autres espèces sont nettement moins tolérantes. Chez les quatre espèces de julides, la durée de tolérance à l'immersion est corrélée de manière significative avec le rapport surface/volume. Toutefois, *Polydesmus denticulatus* reste un cas particulier, montrant une tolérance à la submersion plus élevée. Les mécanismes éventuels de cette capacité sont discutés.

INTRODUCTION

Diplopods are usually supposed to be weak tolerators if they become submerged by rain or inundation (BLOWER, 1955; EISENBEIS & WICHARD, 1985). However, HOFFMAN (1978) reports a diplopod from Papuan caves entering voluntarily the water, ADIS (1986) describes long term submergence in an Amazonian diplopod, and in an investigation of floodplain soil animals the widespread European diplopod *Polydesmus denticulatus* was shown to survive up to 75 days in oxygenated cold water (ZULKA, 1991, 1992).

The present experiment should decide if this is a special adaptation of *Polydesmus denticulatus* to life in flood plains or if diplopods in general are able to withstand submersion longer than previously expected.

ZULKA, K. P., 1996. — Submersion tolerance of some diplopod species. *In:* GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 477-481. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

MATERIAL AND METHODS

Specimens of *Polydesmus denticulatus* C. L. Koch, *Brachyiulus bagnalli* (Brölemann), *Ophyiulus pilosus* (Newport), *Cylindroiulus boleti* (C. L. Koch), and *Leptoiulus proximus* (Némec) were collected by hand in May 1992 in an alder forest near Marchegg, Lower Austria. All these species are widespread in Central Europe and inhabit a vast range of habitats (BLOWER, 1985), but *P. denticulatus* is the only one of them living also in temporarily flooded areas and surviving inundations submerged (ZULKA, 1991). Since the females of *Ophyiulus pilosus* and *Leptoiulus proximus* could not be separated from each other and from the syntopic *Julus scandinavius* with certainty, only males of these two species were used in the experiment. About ten specimens of each species were placed individually into plastic tubes of 2.2 cm diameter and 5.2 cm height that were closed with gauze. The tubes were flooded with aerated water of 9±1°C in a 12 litre-aquarium. Bubbles from an air stone connected to an aquarium pump maintained oxygen saturation in the water as well as slow continuous circulation of the water body. Air bubbles in the tubes trapped beneath the gauze cover were sucked off with a pipette. Oxygen saturation was measured with a WTW oxymeter at the beginning and near the end of the experiment and ranged between 94% and 98%, i. e. around 10.4 mg/l. Typically the animals adhered at the gauze cover. The tubes were checked daily and the animals were removed when their body became elongated (endosmosis) and they were unable to walk anymore.

To estimate the surface-volume ratio of the species, the julids were modelled as cylinders with a surface $S=2\pi r(r+h)$ and volume $V=\pi r^2 h$, leading to a surface-volume ratio $R=2(r+h)/rh$ (r: radius, h: height). However, in *Polydesmus denticulatus* the cylinder model would have underestimated the surface-volume ratio because of the well-developed paranota. Thus, the calculation was based on a cross-section geometry as described in Figure 1 and leads to $S=2\pi r(r+h)+4rh$, $V=4r^2h$, $R=(\pi(r+h)+4rh)/2rh$. For r and h the average values were taken from SCHUBART (1934).

The medians of the submersion times were compared by Kruskal-Wallis ANOVA with subsequent multiple a-posteriori comparisons after CONOVER (1980), see also BORTZ *et al.* (1989), p. 231. The average ranks for every species were tested against:

$$\Delta\bar{R}_{(crit)} = t_{(N-k,\ \alpha/2)} \cdot \sqrt{\frac{N \cdot (N+1)}{12}} \cdot \sqrt{\frac{N-1-H_{emp}}{N-k}} \cdot \sqrt{\frac{1}{N_j} + \frac{1}{N_j'}}$$

RESULTS

Polydesmus denticulatus showed the highest median submersion times of all five species (Fig. 2). However, the difference of the medians between *P. denticulatus* and *B. bagnalli* is not significant (Table 1). The maximal tolerance time in *B. bagnalli* was even higher (Fig. 2) with one individual drowning only after 65 days. The other species are significantly less tolerant. The maximal of survival time in *Ophyiulus pilosus* and *Leptoiulus proximus* are about two weeks. Females generally showed a better performance (Fig. 3), but the differences between sexes were not significant.

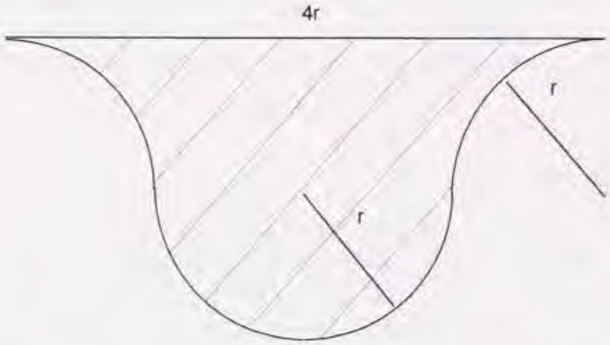


FIG. 1. — Cross-section geometry of *Polydesmus denticulatus* for the calculation of the surface/volume ratio $R=(\pi(r+h)+4rh)/2rh$.

In Figure 3 the median survival time is plotted against the surface-volume ratio R. The values are scattered around the regression line 1 and the correlation between survival time and R is insignificant (r = 0.53). However, if one excludes males and females of *Polydesmus denticulatus* as obvious outliers, the correlation becomes significant (regression line 2, r = 0.88, P<0.05, two-tailed). If one takes only males into consideration, the fit of the regression line gets even better and the correlation becomes highly significant (regression line 3, r = 0.99, P<0,01, two-tailed). This suggests, that in Julidae the survival times are to a high extent determined by the surface/volume ratio: the smaller the species, the higher the submersion tolerance.

Source : MNHN, Paris

TABLE 1. — Multiple *a-posteriori* contrasts after KRUSKAL-WALLIS-ANOVA between species (CONOVER, 1980). n. s. = not significant, * = significant (P<0.05).

	Polydesmus denticulatus	*Brachyiulus bagnalli*	*Cylindroiulus boleti*	*Ophyiulus pilosus*	*Leptoiulus proximus*
Polydesmus denticulatus		n.s.	*	*	*
Brachyiulus bagnalli	n.s.		*	*	*
Cylindroiulus boleti	*	*		*	n.s.
Ophyiulus pilosus	*	*	*		n.s.
Leptoiulus proximus	*	*	n.s.	n.s.	

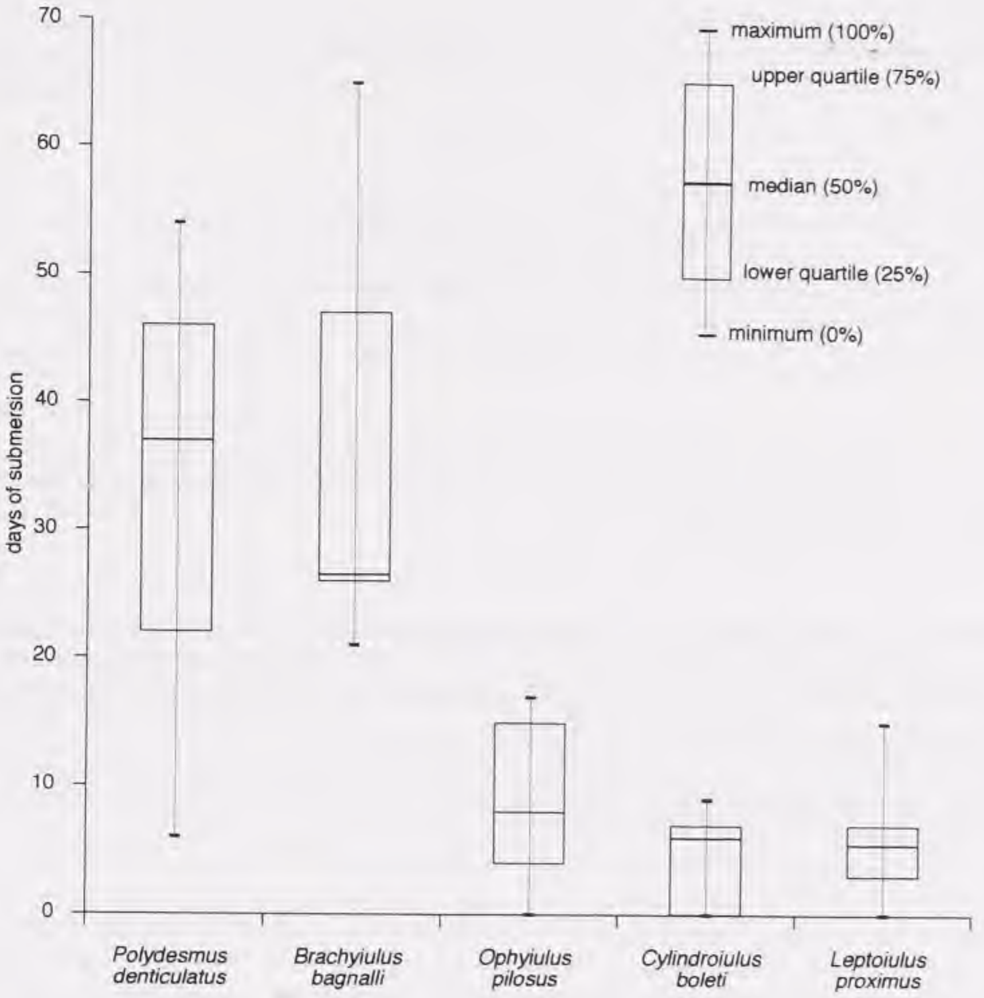


FIG. 2. — Survival times of five diplopod species submerged in water of 9±1°C and 94-98% oxygen saturation.

Source : MNHN, Paris

DISCUSSION

In *P. denticulatus* flooding tolerances are highest. But there are small julids like *B. bagnalli* with survival tolerances of the same magnitude that do not live in flood-prone habitats. So submersion tolerance of adults cannot be the only factor to explain why *P. denticulatus* can live in flooded places and others cannot. The unusual phenology of the species with reproduction in summer (SCHUBART, 1934) or the wide oscillations in population density indicating a high reproductive potential (BLOWER, 1970; ZULKA, 1991) may be additional preadaptations to life in floodplains.

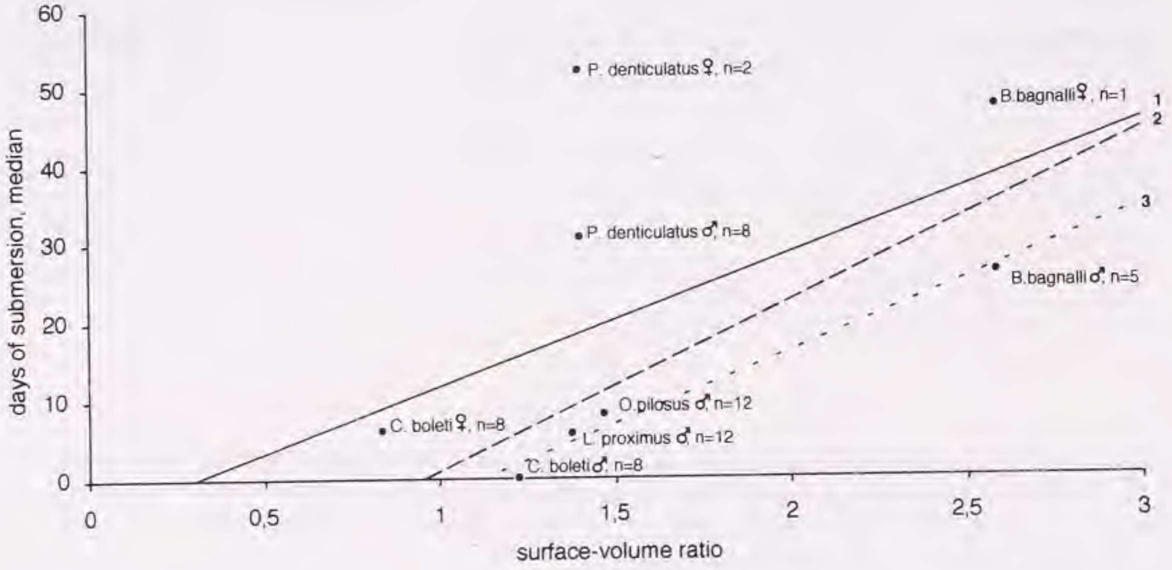


FIG. 3. — Scatter diagram of submersion tolerance times against surface/volume ratio in 5 diplopod species. 1: regression line based on all species and sexes, 2: regression line without *Polydesmus* data, 3: regression line without *Polydesmus* and female data.

In the other investigated julids flooding tolerances differ widely, depending mainly on the size of the species. Since most of them withstand a few days in water, they should be able to survive short time flooding caused by rain but unable to live in frequently inundated places.

Regarding the physiological mechanisms that allow the species a long survival under water, three possibilities could be imagined:

1. The species lives on its anaerobic pathways, and accumulates end products of glycolysis (see survey in CRAWFORD, 1978).

2. Oxygen supply by diffusion over the whole or over parts of the body cuticle is sufficient.

3. There are surface structures that maintain an air cover acting as a plastron. Such structures were found in the tropical millipede *Gonographis adisi* (MESSNER & ADIS, 1988).

In the present experiment the first possibility cannot be excluded, but it is rather unlikely, since the tolerance times are long and *Polydesmus denticulatus* drowns soon when submerged in unsaturated water (ZULKA, 1991).

Source : MNHN, Paris

There are indications for the second possibility at least in julids, since tolerances are highly correlated with surface/volume ratio.

No continuous air film around the body was observed except for the very first time when the animals got under water. When the last air bubbles between the hind edges of the metazonite and the ring duplicatures had already disappeared for a long time they still were active. However, spiracle structures might act as an interface between water and tracheal air, preventing the tracheae from being flooded and enabling plastron respiration. In this case, a similar relationship between tolerances and surface/volume ratio should be expected, since the spiracle area is correlated with the body surface.

Possibly the main oxygen source in all species is cutaneous diffusion, but in *P. denticulatus* special features like spiracle plastron structures (MESSNER, *in litt.*) could enhance the air supply under water. This would explain the higher tolerance values in this species (Fig. 3).

From the present data a clear decision is not possible. A comparison of flooding tolerances among *Polydesmus* species covering a broad range of size classes and living in very different habitat types in the East Alps (TADLER & THALER, 1993) should further elucidate the problem.

ACKNOWLEDGMENTS

I am very indebted to R. L. HOFFMAN and A. TADLER for valuable discussions, to Z. KORSÓS for taxonomic advice regarding *Brachyiulus*, to G. PASS for comments on an earlier version of the manuscript, to G. REIMER and A. TADLER for help during field work, and to G. SCHALLER for supervising the experiment.

REFERENCES

ADIS, J., 1986. — An "aquatic" millipede from a Central Amazonian inundation forest. *Oecologia*, **68** : 347-349.

BLOWER, J. G., 1955. — Millipedes and centipedes as soil animals. *In* : D. K. McE. KEVAN, *Soil Zoology. Proc. Univ. Nottingham Second Easter School Agricultural Science, 1953*. London : 138-151.

BLOWER, J. G. 1970. — The millipedes of a Cheshire wood. *J. Zool. Lond.*, 160 : 455-496.

BLOWER, J. G., 1985. — *Millipedes* (*Synopses of the Br. Fauna* NS, **35**). London, E. J. Brill & W. Backhuys, 242 pp.

BORTZ, J., LIENERT, G. A. & BOEHNKE, K., 1989. — *Verteilungsfreie Methoden in der Biostatistik*. Berlin, Springer Verlag, 939 pp.

CONOVER, W. J., 1980. — *Practical nonparametric statistics*. New York, Wiley.

CRAWFORD, R. M. M., 1978. — Biochemical and ecological similarities in marsh plants and diving animals. *Naturwissenschaften*, **65** : 194-201.

EISENBEIS, G. & WICHARD, W., 1985. — *Atlas zur Biologie der Bodenarthropoden*. Stuttgart, New York, Gustav Fischer, 435 pp..

HOFFMAN, R. L., 1978. — Diplopoda from Papuan caves (Zoological results of the British speleological expedition to Papua-New Guinea, 1975, 4). *Int. J. Speleol.*, **9** : 281-307.

MESSNER, B. & ADIS, J., 1988. — Die Plastronstrukturen der bisher einzigen submers lebenden Diplopodenart *Gonographis adisi* Hoffman 1985 (Pyrgodesmidae, Diplopoda). *Zool. Jb. Anat.*, **117** : 277-290.

SCHUBART, O., 1934. — Tausendfüßler oder Myriapoda I: Diplopoda. *In* : F. DAHL, Tierw. Deutschl. **28**. Jena, G. Fischer, 1-318.

TADLER, A. & THALER, K., 1993. — Genitalmorphologie, Taxonomie und geographische Verbreitung ostalpiner Polydesmida (Diplopoda: Helminthomorpha). *Zool. Jb. Syst.*, **120** : 71-128.

ZULKA, K. P., 1991. — Überflutung als ökologischer Faktor: Verteilung, Phänologie und Anpassungen der Diplopoda, Lithobiomorpha und Isopoda in den Flußauen der March. Dissertation. Wien, Formal- und Naturwiss. Fakultät Univ. 65 pp.

ZULKA, K. P., 1992. — Myriapods from a Central European river floodplain. [*In* : E. Meyer, K. Thaler & W. Schedl, *Advances in Myriapodology*.] *Ber. nat.-med. Verein Innsbruck*, **Suppl. 10** : 189.

Source : MNHN, Paris

Source : MNHN, Paris

Eversible Vesicles in Myriapoda

Frantisek WEYDA

Dept. of Insect Morphology, Institute of Entomology, Branisovska 31,
370 05 Ceske Budejovice, Czech Republic

ABSTRACT

Land arthropods can employ several mechanisms of water uptake. In addition to drinking and water vapour absorption, the atelocerate arthropods (= Tracheata, Antennata: myriapods and insects) frequently possess special organs for capillary water uptake, the eversible vesicles (EVs), segmentally arranged paired sacs situated on the ventral side of the trunk or its part. They are probably functionally analogous to EV-like structures of some Onychophora and Chelicerata. EVs have been studied by various authors since the mid 19th century but their ecological and evolutionary roles are still understood poorly. Comparative study of EVs is important for understanding of some acpects of phylogeny of Onychophora & Arthropoda and their adaptations to terrestrial mode of life. In pauropods SILVESTRI (1902) and TIEGS (1947) described two EV-like structures on the collum. Each of these organs consists of several large cells; no ultrastructural and functionnal data are available. In diplopods EVs are known in a Carboniferous millipede *Euphoberia* (SCUDDER, 1882) as well as in the recent groups (VERHOEFF, 1903; MANTON, 1958; DOHLE, 1988). More than eighty pairs of EVs are present on the limb bases in *Brachycybe lecontii*. Specialized cuticle and transporting epithelium are typical for the absorbing part of an EV of that species. Basic experiments prove that the water absorption from a wet substrate is possible. In chilopods no EVs are developed (see DOHLE, 1988). In symphylans EVs are present in various numbers (HAASE, 1889; TIEGS, 1945; RAVOUX, 1962; DOHLE, 1988); they are usually located on bases of the legs of trunk segments 3-10 but reduction of their number is a common feature. Specialized transporting epithelium is present in the absorbing part of EV, and the water absorption proper has been proved by simple experiments (TIEGS, 1940).

RÉSUMÉ

Vésicules réversibles chez les myriapodes.

Les arthropodes terrestres sont capables de mettre en œuvre plusieurs mécanismes d'hydratation. Outre la capacité d'ingestion d'eau et d'absorption de vapeur, les arthropodes Atelocerata possèdent des organes spéciaux destinés à l'hydratation capillaire, les vésicules réversibles (VR), paires de sacs répartis suivant la segmentation dans la partie ventrale du tronc. Elles ont vraisemblablement une fonction analogue à celle des structures de certains onychophores et chelicérates. Les VR ont été étudiées par divers auteurs depuis le milieu du 19e siècle mais leur rôle écologique évolutif est très mal compris. Une étude comparative de ces vésicules paraît importante pour la compréhension de la phylogénie des onychophores et des arthropodes et de leur adaptation au mode de vie terrestre. Chez les pauropodes on a décrit deux structures semblables aux VR sur le collum. Chacun de ces organes comporte plusieurs grandes cellules ; aucune donnée ultrastucturale ou fonctionnelle n'est disponible. Chez les diplopodes, on les connaît tant chez *Euphoberia*, un diplopode du Carbonifère, que dans les groupes récents. Plus de 80 paires de ces vésicules existent chez *Brachycybe lecontii*. Une cuticule spécialisée et un épithélium de transport constituent les éléments typiques de leur partie absorbante. Les expériences prouvent que l'absorption d'eau à partir d'un substrat humide est possible. Aucune structure de ce genre n'existe chez les chilopodes. Chez les symphyles, elles existent en nombres variés ; elles sont généralement situées à la base des pattes des segments du corps III à X mais la réduction de leur nombre est un caractère fréquent. Un épithélium de transport spécialisé est présent dans la partie absorbante de la vésicule, et l'absorption d'eau a été démontrée par des expériences simples de TIEGS.

WEYDA, F., 1996. — Eversible vesicles in Myriapoda. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 483. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

Source : MNHN, Paris

Étude comparative des techniques d'échantillonnage des macroarthropodes saprophages (Isopoda & Diplopoda)

Etienne BRANQUART *& Charles* GASPAR

Unité de Zoologie générale et appliquée, Faculté des Sciences agronomiques, B-5030 Gembloux, Belgique

RÉSUMÉ

Des peuplements d'isopodes et de diplopodes ont été échantillonnés à l'aide de trois techniques au printemps 1992 dans trente sites forestiers du sud de la Belgique : pièges d'interception, échantillonnage par quadrats et extraction au berlese, collecte manuelle dans les bois morts. Les résultats obtenus sont tout à fait différents car chacune des trois méthodes autorise une collecte préférentielle d'espèces particulières. Les avantages, limites et inconvénients de ces méthodes d'échantillonnage sont mis en évidence et le concept d'activité est discuté en rapport avec la biologie des macroarthropodes saprophages. Des critères en vue du choix d'une méthode sont proposés en accord avec les buts que se fixent les recherches entreprises.

ABSTRACT

Comparative study of the sampling methods for saprophagous macroarthopods (Isopoda and Diplopoda).

Woodlouse and millipede populations have been sampled by three methods in Spring 1992 in thirty forest stands of Southern Belgium: pitfall trapping, berlese extraction and dead wood hand-sorting. The results are quite different because each of the three methods allows a preferential collect of particular species. The advantages, limitations and drawnbacks of these sampling methods are underlined and the concept of activity is discussed compared to saprophagous macroarthropod biology. Criteria for the choice of sampling method are proposed according to the study aims.

INTRODUCTION

Il existe plusieurs techniques d'échantillonnage quantitatif ou semi-quantitatif des populations de macroarthropodes saprophages (isopodes et diplopodes notamment) : (1°) l'échantillonnage par la méthode des quadrats suivi d'une extraction à l'aide d'appareils de type Berlese-Tullgren ou de type Kempson ; (2°) le piégeage par pièges d'interception, encore appelés pièges à fosse ou pièges Barber (= pitfall-traps), qui mesure l'activité ou l'abondance relative des populations ; (3°) des techniques moins usitées de tri manuel ou de chasse à vue, essentiellement qualitatives.

D'après un survol de plus de 50 travaux ayant trait à des inventaires régionaux et à des études biocénotiques, 72% des études reposent sur un échantillonnage par quadrat suivi d'extraction sélective. Ce type de méthodologie semble donc constituer une référence, même s'il

BRANQUART, E. & GASPAR, C., 1996. — Étude comparative des techniques d'échantillonnage des macroarthropodes saprophages (Isopoda & Diplopoda). *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 485-492. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

ne permet pas toujours d'obtenir des résultats exhaustifs et donne des estimations d'abondance biaisées par le rendement parfois déficient des extractions (VAN DER DRIFT, 1951 ; EDWARDS & FLETCHER, 1970).

Des techniques de piégeage sont mises en oeuvre dans 45 % des cas, seules ou en complément à des extractions. Leur emploi relativement commode et peu onéreux ainsi que certaines difficultés inhérentes à l'échantillonnage par quadrat et extraction des populations évoluant sur des sols très superficiels (pelouses calcaires, par exemple) semblent justifier leur utilisation (DAVIS & JONES, 1978 ; VAN ETTEN & ROOS, 1984 ; SIMONSEN, 1985 ; KIME, 1992 ; PEDROLI-CHRISTEN, 1993). Par ailleurs, on sait que les techniques de piégeage sont couramment utilisées pour la capture des arthropodes prédateurs épigés comme les arachnides (MAELFAIT & BAERT, 1975 ; UETZ & UNZICKER, 1976) ou certains groupes de coléoptères (THIELE, 1977 ; BRYAN & WRATTEN, 1984 ; DUFRENE, 1992). L'existence d'une relation entre l'activité de ces arthropodes et leur densité effective constitue par ailleurs un vaste sujet de discussion (e.a. LUFF, 1975 ; ADIS, 1979 ; BAARS, 1979a ; LOREAU, 1984 ; HALSALL & WRATTEN, 1988 ; TOPPING & SUNDERLAND, 1992).

Concernant les macroarthropodes saprophages, les études détaillées permettant de comparer les mesures d'activité résultant de piégeages avec les densités obtenues par quadrat et extraction sont encore rares ou incomplètement exploitées. Ce travail a pour but d'effectuer une étude comparative de différentes techniques d'échantillonnage et de préciser à quoi correspond le concept d'activité au niveau des populations d'isopodes et de diplopodes.

MATÉRIEL & MÉTHODES

Une étude destinée à caractériser les peuplements de la macrofaune saprophage des sols forestiers du Sud de la Belgique (entre Sambre et Meuse) est en cours de réalisation. Des campagnes d'échantillonnage ont été menées simultanément dans 30 sites forestiers représentatifs de la diversité pédologique et phytosociologique de cette région. L'échantillonnage de la faune a été réalisé durant le printemps 1992, suivant 3 techniques différentes, à savoir des quadrats suivis d'extractions au Berlese, des mesures d'activité superficielle ainsi qu'une fouille manuelle du bois mort. Des échantillons de sol (litière + sommet de l'horizon humifère) ont été prélevés sur 6 quadrats de 625 cm^2 dans chacun des sites étudiés et extraits durant 3 semaines. Le choix d'une surface unitaire de 625 cm^2 tient compte à la fois de la taille, de la densité moyenne et du taux d'agrégation des animaux étudiés (SUTTON, 1972; BLOWER, 1985; DAVID, 1988). Trois pièges d'activité ont été installés par station. Il s'agit de pots transparents en P.E.T. de 8 cm de diamètre, contenant une solution diluée de formol, additionnée de quelques gouttes de détergent inodore (TEEPOL) [DUFRENE, 1988]. Quant au bois mort, il a été fouillé minutieusement dans chaque station suivant un effort de chasse constant (2 x 1/2 h par site).

L'efficacité relative des différentes techniques d'échantillonnage vis-à-vis de chacune des 30 espèces de macroarthropodes rencontrés durant cette étude (13 espèces d'isopodes et 17 espèces de diplopodes) a été évaluée par le calcul de 2 indices différents. Le premier, appelé *indice d'efficacité relative*, exprime la fréquence d'occurrence de chaque espèce échantillonnée par 3 méthodes différentes : le piégeage, l'extraction et la recherche manuelle dans le bois mort. Le calcul de cet indice a permis un groupement des espèces suivant leur aptitude à être échantillonnées par chacune des 3 techniques.Les groupes proposés ont été créés par la méthode "k-means", suivant l'algorithme de groupement agglomératif proposé par HARTIGAN & WONG (1979), disponible dans le logiciel SYSTAT.

Comme les valeurs attribuées à l'efficacité relative des différentes techniques d'échantillonnage sont susceptibles de varier suivant l'intensité avec laquelle ces dernières ont été mises en oeuvre, elles ont été affinées par le calcul de l'*indice d'efficacité du piégeage* (ou indice d'activité) proposé par BRANQUART *et al.* (1995). Celui-ci permet une comparaison de l'activité (résultats des piégeages) et de la densité (résultats des extractions) de la faune saprophage sur une base quantitative. La valeur de cet indice a été calculé en considérant de manière globale le "peuplement" des 30 stations; pour chaque taxon, l'indice d'activité mesure le rapport de l'abondance relative estimée par extraction et par piégeage:

$$Ie = 2 \times [(nP/NP)/((nP/NP) + (nE/NE))] - 1$$

où nP et nE symbolisent le nombre d'individus d'une espèce échantillonnés respectivement par piégeage et par quadrat/extraction alors que NP et NE correspondent au nombre total d'isopodes et de diplopodes échantillonnés par les mêmes techniques.

Source : MNHN, Paris

RÉSULTATS ET DISCUSSION

Nous avons d'abord cherché à savoir s'il existait une technique qui permette un échantillonnage exhaustif de la richesse spécifique globale propre à un site, celle-ci étant caractérisée, dans le cas présent, par le nombre d'espèces échantillonnées par au moins l'une des trois techniques utilisées. Dans les différentes stations, le nombre de taxons capturés par piégeage, par quadrat-extraction et par chasse à vue dans le bois mort a été comparé au nombre total d'espèces présentes (Fig. 1). Pour chacune des 3 techniques, on trouve une corrélation très élevée ($P < 0.001$) entre le nombre d'espèces capturées par un seul type d'échantillonnage et le nombre total d'espèces présentes dans un site. La pente de chacune des 3 droites ajustées diffère significativement de 1 ($b_{\text{Piégeage}} = 0{,}85$; $b_{\text{quadrat-extraction}} = 0{,}65$; $b_{\text{recherche manuelle}} = 0{,}44$), ce qui signifie qu'aucune technique ne permet de recenser tous les taxons présents dans un site donné. On constate cependant que le piégeage se montre globalement plus efficace que les 2 autres techniques pour la recherche de la richesse spécifique globale.

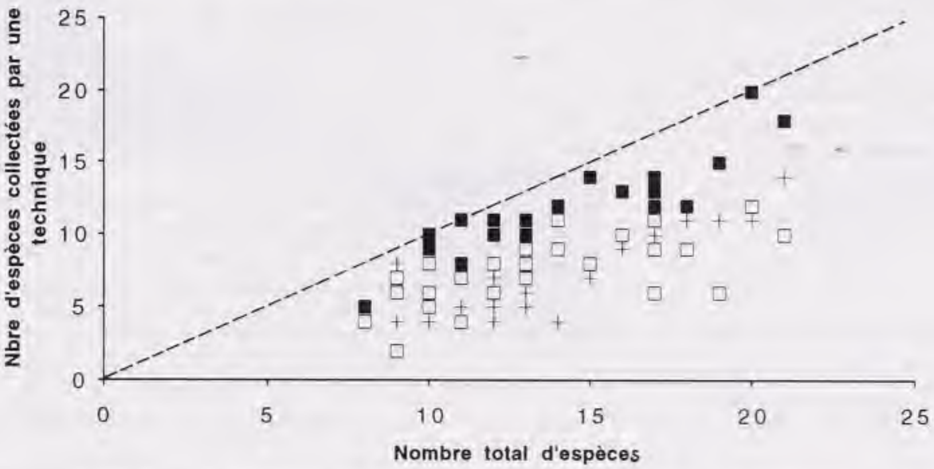


FIG. 1. — Comparaison du nombre d'espèces de macroarthropodes saprophages échantillonnées par piégeage (carrés noirs), par extraction (signes "+") et par recherche manuelle dans le bois mort (carrés blancs) avec le nombre total d'espèces collectées par les 3 techniques dans un même site (diversité stationnelle).

FIG. 1. — Comparison of the number of saprophagous macroarthropods sampled by pitfall traps (black squares), berlese extraction (symbol"+") and hand-sorting of dead wood (white squares) with the total number of species found in each stand".

Afin de savoir si certaines espèces ne sont pas échantillonnées préférentiellement par l'une ou l'autre technique, les 2 indices d'efficacité définis plus haut ont été calculés pour les différentes espèces. La projection des 30 taxons de macroarthropodes saprophages dans un système de coordonnées triangulaires suivant les valeurs de leur indice d'efficacité relative pour les 3 techniques d'échantillonnage (Fig. 2) montre que celles-ci sont fortement sélectives. Globalement, 4 groupes de taxons peuvent être définis (Tableau 1) :

- le *groupe 1*, constitué de petites espèces au mode de vie endogé, bien représentées dans les sols calcimorphes; celles-ci ne sont bien échantillonnées que par quadrat et extraction ;

- le *groupe 2,* constitué d'espèces très mobiles, souvent peu représentatives des milieux forestiers, essentiellement capturées par piégeage ;

- le *groupe 3,* composé de taxons à comportement corticole bien marqué (efficacité relative de la recherche dans le bois mort supérieure à 35 %), généralement bien récoltés par piégeage et beaucoup moins par quadrat-extraction ;

- le *groupe 4,* formé d'espèces collectées préférentiellement par piégeage et par quadrat-extraction, se rencontrant rarement dans le bois mort : il s'agit de taxons qui présentent une

Source : MNHN, Paris

importante activité de surface et vivent essentiellement dans la litière et à l'interface entre celle-ci et l'horizon humifère.

TABLEAU 1. — Présentation des 4 groupes de taxons, définis d'après leur mode préférentiel d'échantillonnage. L'interprétation donnée à chaque groupe est fournie dans le texte.
TABLE 1. — Four taxonomic groups, related to the preferential sampling technique. Interpretation in the text.

GROUPE 1			GROUPE 2		
HM	*Haplophthalmus mengei*	(Zaddach, 1844)	AO	*Armadillidium opacum*	(C.L. Koch, 1841)
MP	*Macrosternodesmus palicola*	Brôlemann, 1908	AV	*Armadillidium vulgare*	(Latreille, 1804)
SC	*Stygioglomeris crinata*	(Brôlemann, 1913)	JS	*Julus scandinavius*	Latzel, 1884
TH	*Trichoniscoides helveticus*	(Carl, 1908)			
GROUPE 3			**GROUPE 4**		
APi	*Armadillidium pictum*	Brandt, 1833	AN	*Allaiulus nitidus*	(Verhoeff, 1891)
APu	*Armadillidium pulchellum*	(Zenker, 1798)	CS	*Chordeuma silvestre*	C. L. Koch, 1847
CR	*Craspedosoma rawlinsii*	Leach, 1815	GH	*Glomeris hexasticha*	Brandt, 1833
CP	*Cylindroiulus punctatus*	(Leach, 1815)	GM	*Glomeris marginata*	(Villers, 1789)
NV	*Nemasoma varicorne*	C. L. Koch, 1847	LH	*Ligidium hypnorum*	(Cuvier, 1792)
OA	*Oniscus asellus*	Linne, 1758	LK	*Leptoiulus kervillei*	(Brôlemann, 1896)
PMt	*Porcellio monticola*	Lereboullet, 1853	LS	*Leptoiulus simplex* ssp.	(Verhoeff, 1894)
PS	*Porcellio scaber*	(Latreille, 1804)	MG	*Melogona gallicum*	(Latzel, 1884)
PA	*Polydesmus angustus*	Latzel, 1884	OP	*Orthochordeumella pallida*	(Rothenbûhler, 1899)
TN	*Tachypodoiulus niger*	(Leach, 1815)	PD	*Polydesmus denticulatus*	C. L. Koch, 1847
			PM	*Philoscia muscorum*	(Scopoli, 1763)
			PC	*Porcellium conspersum*	Koch, 1841
			TP	*Trichoniscus pusillus*	Brandt, 1833

Il apparaît que les espèces corticoles sont généralement mieux capturées par piégeage que par quadrat-extraction. L'efficacité relative moyenne est plus élevée pour le piégeage (42%) que pour l'extraction (31%) ou pour la recherche dans le bois mort (27%).

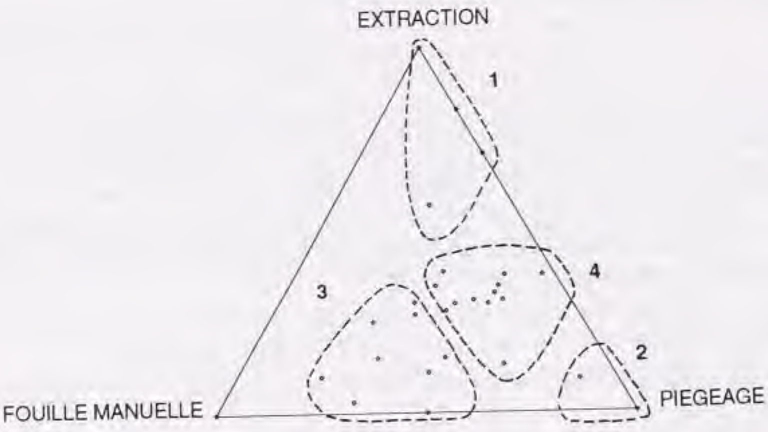


FIG. 2. — Efficacité relative des 3 techniques d'échantillonnage (piégeage, extraction et recherche dans le bois mort) vis-à-vis de 30 espèces de macroarthropodes saprophages. Groupement des taxons suivant leur aptitude à être échantillonnés par ces différentes techniques.

FIG. 2. — Relative efficience of the three sampling methods (pitfall-trapping, funnel-extraction and hand-collecting in the decaying woods) towards 30 saprophagous macroarthropod species. Grouping of the taxa after their ability to be sampled by these different methods.

La Figure 3 illustre la valeur de l'indice d'efficacité du piégeage (ou indice d'activité) pour les adultes de 25 espèces ainsi que pour les juvéniles de 5 familles de diplopodes. Cet indice est calculé sur un total de 3784 individus obtenus par piégeage et 1769 par extraction. A nouveau,

Source : MNHN, Paris

les abondances cumulées des macroarthropodes saprophages offrent une image très différente du peuplement suivant la technique d'échantillonnage utilisée. Le peuplement global “Berlese”, moins diversifié, est essentiellement dominé par une petite espèce d'Isopode, *Trichoniscus pusillus*, qui représente plus de 50% des effectifs totaux. Y sont également bien représentées les petites espèces endogées du groupe 1 ainsi que tous les stades juvéniles des diplopodes. En revanche, le peuplement global résultant des piégeages est beaucoup plus équilibré et diversifié. Il est dominé par des individus adultes appartenant aux grandes espèces mobiles des groupes 2 et 3. Plusieurs de ces espèces présentent des pics d'activité ponctuels très marqués dans le temps, probablement liés à l'activité sexuelle car les captures comprennent une forte proportion d'individus mâles : c'est le notamment le cas de *Craspedosoma rawlinsii*, *Ligidium hypnorum*, *Polydesmus denticulatus* et *Tachypodoiulus niger*.

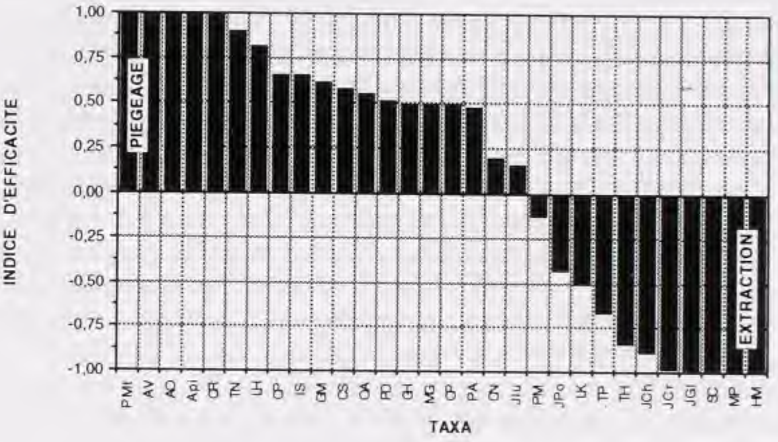


FIG. 3. — Valeurs de l'indice d'efficacité du piégeage pour différents taxons (abscisse). La signification des symboles est reprise au Tableau 1, à l'exception de JIu, JPo, JCh, JCr et JGl qui correspondent respectivement aux juvéniles de Iulides, de Polydesmides, de Chordeumatides, de Craspédosomatides et de Glomérides.

FIG. 3. — Trappability of the taxa. For symbols, see Table 1 except for JIu, JPo, JCh, JCr and JGl that correspond respectively to juveniles of Julida, Polydesmida, Chordeumatidea, Craspedosomatidea and Glomerida.

Rappelons que les résultats exposés ci-dessus ne se rapportent qu'à une seule saison d'échantillonnage (le printemps) et sont *a priori* susceptibles de varier en fonction de la période de prélèvement et du type de milieu étudié. Cependant, on notera que les valeurs de l'indice d'efficacité du piégeage correspondent très bien avec celles qui ont été calculées sur un laps de temps plus important dans une étude antérieure effectuée dans la même région ($r = 0{,}925$; $P < 0{,}001$) (BRANQUART *et al.*, 1995). Les valeurs de cet indice, calculées durant les périodes d'activité des animaux, semblent donc correspondre à une caractéristique intrinsèque des taxons étudiés.

Au vu de ces résultats, il apparaît clairement que l'efficacité relative des différentes techniques d'échantillonnage ou de capture dépend de l'écologie des taxons et du stade de développement des individus. Les *abondances mesurées par quadrat-extraction* donnent une bonne image de la densité des espèces dominantes vivant dans la litière et dans les premiers centimètres de l'horizon humifère. En outre, elles conduisent à une estimation fiable de l'abondance de la plupart des stades de développement, à l'exception des tous jeunes individus (DAVID, 1988). Cependant, ce type d'échantillonnage est susceptible de donner des résultats largement sous-estimés lorsqu'il est pratiqué en dehors des périodes d'activité des macroarthropodes. Ainsi, durant les périodes critiques de sécheresse ou de gel, bon nombre d'espèces s'enfoncent verticalement dans le sol ou se regroupent dans des micro-sites particuliers, sous les pierres, dans le bois mort et les plages de mousse et échappent ainsi à l'échantillonnage (SUTTON, 1972 ; GEOFFROY, 1981). De plus, il faut souligner que l'indice de dispersion variance/moyenne des arthropodes étudiés est presque toujours supérieur à 2. Les

Source : MNHN, Paris

dispersion variance/moyenne des arthropodes étudiés est presque toujours supérieur à 2. Les estimations d'abondance s'accompagnent donc souvent d'un coefficient de variation assez important, même lorsque le nombre d'échantillons unitaires augmente. Même si on considère habituellement que les extractions réalisées avec des appareils de type Berlese-Tullgren donnent des résultats reproductibles (GEOFFROY *et al.*, 1981), on devra toujours avoir à l'esprit les différentes sources d'erreur associées à l'estimation des densités de macroarthropodes. Celles-ci découlent d'une part, de la distribution fortement agrégative des organismes, de leurs migrations saisonnières, des rythmes nycthéméraux d'activité et, d'autre part, des caractéristiques inhérentes à la technique utilisée.

Les *mesures d'activité* se rapportent essentiellement à des individus adultes ou subadultes qui se déplacent activement à la surface du sol. Ce type de capture permet en outre de récolter les espèces présentes en plus faible densité ou des taxons montrant une préférence pour le bois mort. Du fait de sa bonne efficacité relative pour la majorité des taxons et de son fonctionnement en continu, le piégeage permet de réaliser à peu de frais un inventaire qualitatif assez complet des populations d'isopodes et de diplopodes présentes dans un site déterminé. Cet avantage a déjà été souligné pour d'autres groupes taxonomiques comme les arachnides (UETZ & UNZICKER, 1976 ; TOPPING & SUNDERLAND, 1992) et les carabides (THIELE, 1977). On notera cependant qu'il arrive de récolter dans les pièges de type Barber des individus de passage, appartenant à des formes très mobiles peu caractéristiques du site étudié (julides, polydesmides, armadillidiides). Cet effet est d'ailleurs susceptible de s'accentuer dans les habitats défavorables, où l'activité locomotrice des arthropodes augmente fortement (GRUM, 1971 ; BAARS, 1979b). En outre, on a montré que l'efficacité relative du piégeage est éminemment variable d'un taxon à l'autre : elle dépend à la fois de l'"agilité" des individus (SUTTON, 1972), c'est-à-dire de leur faculté à repérer et à éviter le piège, ainsi que de leur pouvoir de dispersion (BLOWER, 1969), en relation avec la taille, la mobilité et le taux d'agrégation au sein de la population. A ce propos, il semble que les taxons vivant dans le bois mort, au moins durant une partie de leur cycle de développement (groupe 3), forcément répartis de manière agrégative, soient caractérisés par un pouvoir de dispersion important, comme en attestent les valeurs prises par l'indice d'efficacité du piégeage. On notera encore que l'efficacité relative du piégeage est bien meilleure pour les groupes prédateurs, tels que les carabides, les chilopodes ou certains arachnides, que pour les espèces saprophages, relativement moins mobiles.

Au cours d'un cycle de piégeage annuel réalisé dans les forêts feuillues du sud de la Belgique, BRANQUART *et al.* (1995) ont montré que les macroarthropodes saprophages présentent en général deux périodes marquées d'activité de surface, séparées par deux phases de repos. La première est induite par la sécheresse estivale (éventuellement accompagnée de phénomènes de diapause), la seconde est déclenchée par le froid hivernal (cf. GEOFFROY & CÉLÉRIER, ce volume). Ceci s'accorde assez bien avec les travaux de BARLOW (1957) et de CLOUDSLEY-THOMPSON (1988) qui ont montré que l'activité des isopodes et des diplopodes est essentiellement régulée par les conditions climatiques. En particulier, l'activité trophique de ces animaux est très nettement régulée par la température, l'humidité du substrat et la photopériode (VAN DER DRIFT, 1975 ; DAVID, 1987 ; GEOFFROY *et al.*, 1987 ; MOCQUARD *et al.*, 1987). De plus, le pic d'activité le plus important est généralement situé au printemps, et semble correspondre à l'activité de reproduction des animaux (recherche de partenaires et de sites de ponte) (BANERJEE, 1979). En conséquence, durant les périodes d'activité autorisées par des conditions climatiques favorables, les macroarthropodes saprophages partagent leur temps entre leur activité sexuelle et leur activité trophique. On pourrait donc formuler l'hypothèse que le niveau d'activité des isopodes et des diplopodes enregistré par piégeage est proportionnel au rôle joué dans la décomposition de la matière organique tout comme, chez les carabes, le concept de "densité d'activité" est souvent relié à l'intensité de l'activité prédatrice (THIELE, 1977).

On peut enfin se poser la question de savoir s'il existe une relation entre la densité et le niveau d'activité des différents taxons. BRANQUART *et al.* (1995) ont montré qu'une relation de

Source : MNHN, Paris

ce type ne pouvait être vérifiée que pour les espèces bien échantillonnées par quadrat-extraction et par piégeage (groupe 4), à la condition que le piégeage soit réalisé, sinon au cours d'un cycle annuel complet, du moins durant les phases majeures d'activité des animaux, en accord avec les études de BAARS (1979a) et de LUFF (1982) pour les carabides.

CONCLUSION

Le choix d'une technique d'échantillonnage des populations de macroarthropodes saprophages édaphiques doit toujours être déterminé par le but de l'étude (Tableau 2). Dans tous les cas, les mesures d'activité devront être interprétées avec prudence, étant donné qu'elles dépendent à la fois de l'abondance des populations, du degré d'activité des individus qui les composent ainsi que de leur l'agilité. Ainsi, on pourra comparer valablement le niveau d'activité de plusieurs populations d'une même espèce, échantillonnées simultanément dans des conditions aussi similaires que possible. Le piégeage pourra être utilisé avantageusement dans le cadre de la réalisation d'atlas ou de campagnes de surveillance faunistique et, en complément aux méthodes d'extraction, pour comparer des peuplements provenant de différents écosystèmes. L'échantillonnage par quadrats suivi d'extraction s'appliquera davantage dans le cadre d'études biocénotiques ou de dynamique de populations, car il permet de récolter l'ensemble des stades de développement. En milieu forestier, il devra néanmoins toujours être complété par un échantillonnage du bois mort par fouille manuelle ou par extraction afin d'obtenir une image aussi complète que possible des peuplements étudiés.

TABLEAU 2. — Choix d'une technique d'échantillonnage en fonction du type d'étude.
TABLE 2. — Choice for a sampling technique in relation to the study.

	PIEGEAGE	QUADRAT-EXTRACTION
Inventaires régionaux	**	*
Etudes de peuplements	*	**
Etudes biocénotiques		**
Dynamique de population		**
Mesures d'activité	**	

REMERCIEMENTS

Ce travail a été subventionné par un financement I.R.S.I.A. Nous exprimons ici nos remerciements aux sociétés anonymes Spa (groupe Spadel) et Chaudfontaine Monopole qui ont fourni gracieusement les bouteilles en P.E.T. nécessaires à la réalisation des pièges d'interception.

RÉFÉRENCES

ADIS, J., 1979. — Problems of interpreting arthropod sampling with pitfall traps. *Zool. Anz.*, **202** : 177-184.

BAARS, M., A., 1979a. — Catches in pitfall traps in relation to mean densities of Carabid Beetles. *Oecologia (Berl.)*, **41** : 25 - 46.

BAARS, M. A., 1979b. — Patterns of movement of radioactive Carabid Beetles. *Oecologia (Berl.)*, **44** : 125-140.

BANERJEE, B., 1979. — Diurnal and seasonal variations in the activity of the millipedes *Cylindroiulus punctatus* (Leach), *Tachypodoiulus niger* (Leach) and *Polydesmus angustus* Latzel. *Oikos*, **18** : 141-144.

BARLOW, C. A., 1957. — A factorial analysis of distribution in three species of Diplopods. *Tijdschr. Entom.*, **100** : 349-426.

BLOWER, J. G., 1969. — Age-structure of millipede populations in relation to activity and dispersion. *In* : J. G. SHEALS, *The soil ecosystem*, London : 209-205.

BLOWER, J. G., 1985. — *Millipedes* (*Synopses of the Br. Fauna* NS, **35**). London, E. J. Brill & W. Backhuys, 242 pp.

BRANQUART, E., KIME, R. D., DUFRENE, M., TAVERNIER J. & WAUTHY, G., 1995. — Macroarthropod-habitat relationships in oak forests in South Belgium. 1. Environment and communities. *Pedobiologia*, **39** : 243-263.

BRYAN, K. M. & WRATTEN, S. D., 1984. — The response of polyphagous predators of prey spatial heterogeneity; aggregation by carabid and staphylinid beetles to their cereal aphid prey. *Ecological Entomology*, **9** : 251-259.

Source : MNHN, Paris

CLOUDSLEY-THOMPSON, J. L., 1988. — *Evolution and Adaptation of Terrestrial Arthropods*. Berlin, Springer-Verlag, 141 pp.

DAVID, J. F., 1987. — Consommation annuelle d'une litière de chêne par une population adulte du Diplopode *Cylindroiulus nitidus*. *Pedobiologia*, **30** : 299-310.

DAVID, J. F., 1988. — Les peuplements de Diplopodes d'un massif forestier tempéré sur sols acides. Thèse Doctorat d'état ès-Sciences Naturelles, Muséum National d'Histoire Naturelle & Université de Paris VI, 225 pp.

DAVIS, B. N. K. & JONES, P. E., 1978. — The ground arthropods of some chalk and limestone quarries in England. *Journal of Biogeography*, **5** : 159-171.

DUFRENE, M., 1988. — Description d'un piège à fosse original, efficace et polyvalent. *Bull. Annls Soc. r. belge Ent.*, **124** : 282-285.

DUFRENE, M., 1992. — Biogéographie et Ecologie des Communautés de *Carabidae* en Wallonie. Thèse Doct. Sciences, Université Catholique de Louvain.

EDWARDS, C. A. & FLETCHER, K. E., 1970. — Assessment of terrestrial invertebrate populations. *In* : J. PHILLIPSON, *Methods of study in soil ecology*, Paris, UNESCO : 57-66.

GEOFFROY, J. J., 1981. — Etude d'un écosystème forestier mixte. - V. Traits généraux du peuplement de Diplopodes édaphiques. *Rev. Ecol. Biol. Sol*, **18** : 357-372.

GEOFFROY, J. J., CHRISTOPHE, T., MOLFETAS, S. & BLANDIN, P., 1981. - Etude d'un écosystème forestier mixte. - III : Traits généraux du peuplement de macroarthropodes édaphiques. *Rev. Ecol. Biol. Sol*, **18** : 39-58.

GEOFFROY, J. J., CELERIER, M. L., GARAY, I., RHERISSI, S. & BLANDIN, P., 1987. — Approche quantitative des fonctions de transformation de la matière organique par des macroarthropodes saprophages (Isopodes et Diplopodes) dans un sol forestier à moder. Protocoles expérimentaux et premiers résultats. *Rev. Ecol. Biol. Sol*, **24** : 573-590.

GRUM, L., 1971. — Spatial differentiation of the *Carabus* L. (Col., Carabidae) mobility. *Ekol. Pol.*, **19** : 1-34.

HALSALL, N. G. & WRATTEN, S. D., 1988. — The efficiency of pitfall trapping for polyphagous predatory Carabidae. *Ecological Entomology*, **13** : 293-299.

HARTIGAN, J. A. & WONG, M. A., 1979. — A K-means clustering algorithm : Algorithm AS 136. *Applied Statistics*, **28** : 126-130.

KIME, R. D., 1992. — On abundance of west-european millipedes. *Ber. nat.-med. Verein Innsbruck*, **suppl. 10** : 393-399

LOREAU, M., 1984. — Population density and biomass of Carabidae (Coleoptera) in a forest community. *Pedobiologia*, **27** : 269-278.

LUFF, M. L., 1975. — Some features influencing the efficiency of pitfall traps. *Oecologia* (Berl.), **19** : 345-357.

LUFF, M. L., 1982. — Population dynamics of Carabidae. *Ann. Appl. Biol.*, **101** : 164-170.

MAELFAIT, J. P. & BAERT, L., 1975. — Contribution to the knowledge of the Arachno- and Entomofauna of different woodhabitats. - Part I : sampled habitats theoretical study of the pitfall method; survey of the captured taxa. *Biol. Jb. Dodonea*, **43** : 179-196.

MOCQUARD, J. P., JUCHAULT, P., JAMBU, P. & EUSTEL, E., 1987. — Essai d'évaluation du rôle des crustacés oniscoïdes dans la transformation des litières végétales dans une forêt feuillue de l'ouest de la France. *Rev. Ecol. Biol. Sol*, **24** : 311-327.

PEDROLI-CHRISTEN, A., 1993. — *Faunistique des mille-pattes de Suisse (Diplopoda)*. Documenta faunistica helvetiae 14, Neuchâtel, Centre suisse de cartographie de la faune, 167 pp. + annexes.

SIMONSEN, A., 1985. — Interspecific association among millipeds from western and south-eastern Norway. *Fauna norv. Ser. B*, **32** : 42-44.

SUTTON, S. L., 1972. — *Invertebrates types*. London, Woodlice. Ginn & Company Ltd, 144 pp.

THIELE, H. U., 1977. — *Carabid beetles in their environments*. Berlin, Springer-Verlag, 369 pp.

TOPPING, C. J. & SUNDERLAND, K. D., 1992. — Limitations to the use of pitfall traps in ecological studies examplified by a study of spiders in a field of winter wheat. *J. Appl. Ecology*, **29** : 485-491.

UETZ, G. W. & UNZICKER J. D., 1976. — Pitfall trapping in ecological studies of wandering spiders. *J. arachnol.*, **3** : 101-111.

VAN DER DRIFT, J., 1951. — Analysis of the animal community in a beech forest floor. *Tijdschr. Entomol.*, **94** : 1-168.

VAN DER DRIFT, J., 1975. — The significance of the millipede *Glomeris marginata* (Villers) for oak-litter decomposition and an approach of its part in energy flow. *In* : J. VANEK, *Progress in soil zoology*. The Hague : 293-298.

VAN ETTEN, J. & ROOS, M., 1984. — De invertebratenfauna van de Zuidlimburgse kalkgraslanden : Landpissebeden (Crustacea : Isopoda : Oniscoidea), *Natuurhist. Maandblad.*, **73** : 5 -12.

Source : MNHN, Paris

Experimental Behaviour of a Tropical Invertebrate: *Epiperipatus biolleyi* (Onychophora: Peripatidae)

Julián MONGE-NÁJERA, *Zaidett* BARRIENTOS & *Flanklin* AGUILAR

Biología Tropical, Universidad de Costa Rica, Costa Rica

ABSTRACT

Several aspects of the basic behaviour of *Epiperipatus biolleyi* Bouvier have been studied experimentally in the laboratory. The main preliminary results are presented in this short paper.

RÉSUMÉ

Comportement expérimental d'un invertébré tropical : *Epiperipatus biolleyi* (Onychophora : Peripatidae).

Divers aspects du comportement de *Epiperipatus biolleyi* Bouvier ont été étudiés expérimentalement en laboratoire. Quelques résultats préliminaires sont présentés dans cette courte note.

INTRODUCTION

The limited knowledge on the behaviour of living onychophorans is based on casual observations (RUHBERG, 1985). Quantitative experimental data are currently limited to feeding behavior in one species (READ & HUGHES, 1987) and pheromonal function of crural glands in another (ELLIOTT *et al.*, 1993). This short paper presents the results of controlled experiments on the general behaviour of *Epiperipatus biolleyi* Bouvier collected in Coronado, Costa Rica.

PRELIMINARY RESULTS

In choice tests of natural substrates in the field, for unknown reasons bryophyte vegetation and the soil associated with it were preferred to grass and its soil. In the field, *E. biolleyi* is usually found in the moss-substrate interface and in burrows in the soil. Under experimental conditions, they stayed mainly in the vegetation and rarely in the interface or within the soil. This difference between the laboratory and the field may be due to the fact that *Marchantia* and grass were used, instead of the moss which is also common in the area and provides hiding places for the animals.

In the laboratory this species was unable to form burrows (N=20) suggesting that, in the field, they need natural openings on the substrate during daytime. Their feeding and mating grounds are possibly limited by this factor. Individuals did not show any fidelity to a particular burrow when given the choice of four identical burrows and within 87 hours they switched burrows almost three times. This suggests that they show an opportunistic behaviour, entering

MONGE - NAJERA, J., BARRIENTOS, Z. & AGUILAR, F., 1996. — Experimental behaviour of a tropical invertebrate: *Epiperipatus biolleyi* (Onychophora: Peripatidae). *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 493-494. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

any burrow found nearby when the "resting" time approaches. Most animals enter burrows by walking foward (N=31) but could also enter backwards. They show a tendency to "rest" facing the burrow's entrance, possibly to speed reaction to enemies and climatic factors, as well as to detect passing prey.

No aggressive behaviour for limited burrows was observed. Pairs of animals were seen to rest with some body contact about half of the time, possibly to reduce desiccation and thermic stress. The seven basic resting body postures identified which we called: *Line,* when the body is straight,U shape, S shape, J shape (head) and J shape *(tail), Roll* and *Ring*, were displayed with decreasing frequency by animals in burrows. The frequency of display differs between animals on the surface and those in burrows and there is a slight tendency for the S position to be more frequent for animals in the surface than in the burrows, in which there is a tendency for the U position to occupy the second place in frequency. Onychophoran body posture has not been studied previously, with the exception of reports about coiling or shortening in response to dessication or touch (RUHBERG, 1985).

E. biolleyi hide from light of wave lenght between 470 and 600 nm. Perhaps onychophorans lack the ability to detect light in the infrared and ultraviolet range (MONGE-NÁJERA, 1991).

On freshwater, these animals floated and became slightly turgid after the 25 mn. that the test lasted (N=5). They remained in good health after the test, in contrast to those floated on sea water (N=4), which died after 14-18 mn. (test suspended). This suggests that onychophorans could survive contact with water while transported over freshwater (e.g. during floods), but that dry places are required in natural rafts during possible dispersal across sea (see MONGE-NÁJERA, 1995).

E. biolleyi produces an adhesive lacking smell and colour. When fresh it tastes bitter to a vertebrate predator (i.e. humans, N=9). This is in agreement with the idea that the adhesive evolved originally for defense (MONGE-NÁJERA, 1995). The bird *Turdus grayi* and the snake *Micrurus hemprichii* feed on onychophorans in nature but this fact has hitherto remained unknown to workers in this field because the reports appeared in herpethological and ornithological publications.

In captivity and with a constant food supply, *E. biolleyi* survives for up to 150 days. A marked retraction of the antennae, which become flaccid and curved downwards (sometimes crossed in an X), and elimination of saliva, adhesive substance, faeces and sometimes immature embryos are all indications that the animal is severely stressed. Faeces have small rounded corpuscles which may contain excretory crystals or coccus type bacteria. The species avoids daylight and even weak wind currents. It moults every 15 days (N=7). The mean speed of locomotion away from a light source was 1.1-3 cm/s.

AKNOWLEDGEMENTS

We are grateful to William LAMAR (University of Texas), Alejandro SOLÓRZANO and Esther DOMÍNGUEZ (Universidad de Costa Rica), Wolfgang BOCKELER (University of Kiel) and Hilke RUHBERG (University of Hamburg).

REFERENCES

ELIOTT, S., TAIT, N. N. & BRISCOE, D. A., 1993. — A pheromonal function for the crural glands of the onychophoran *Cephalofovea tomahmontis* (Onychophora: Peripatopsidae). *J. Zool., Lond.*, **231** : 1-9.

MONGE-NÁJERA, J., 1991. — An evolutionary interpretation of fertilization patterns in the Onychophora. *Onych. Newsl.*, **3** : 2-4.

MONGE-NÁJERA, J., 1995. — Phylogeny, biogeography and reproductive trends in the Onychophora. *Zool. J. Linn. Soc.*, **114** : 21-60.

READ, V. M. S. J. & HUGHES., R. N., 1987. — Feeding behaviour and prey choice in *Macroperipatus torquatus* (Onychophora). *Proc. R. Soc. Lond. B*, **230** : 483-506.

RUHBERG, H., 1985. — Die Peripatopsidae (Onychophora). Systematik, Ökologie, Chorologie und phylogenetische Aspekte. *Zoologica* , **137** : 1-183.

Source : MNHN, Paris

Scolopendra morsitans Linnaeus, 1758: a Characteristic Prey of the African Carpet Viper *Echis ocellatus* Stemmler, 1970

***Pascal* Revault**

ORSTOM BP 182 Ouagadougou 01, Burkina Faso

ABSTRACT

This short paper deals with the relationships between *Echis ocellatus*, the African Carpet Viper, which contributes largely to human envenomation, and its chilopodan prey, *Scolopendra morsitans*.

RÉSUMÉ

***Scolopendra morsitans* Linné, 1758 : une proie caractéristique de la vipère africaine *Echis ocellatus* Stemmler, 1970.**

En zone soudano-sahélienne, les vipéridés du genre *Echis* sont responsables d'une grande partie des envenimations humaines (Habib, 1992). La prédation jouant un rôle majeur dans la dynamique et l'organisation des peuplements de reptiles tropicaux (Barbault, 1991), il est intéressant de connaître leur régime alimentaire. 47 *Echis ocellatus* ont été récoltés, dont 37 en octobre 1992 et 8 en avril 1993, dans quatre localités situées autour de Ouagadougou (Burkina Faso) ; fixés dans du formol à 10%, ils ont été disséqués et conservés dans de l'alcool à 60°. 8 individus avaient un tube digestif vide. Chez les 39 autres, on trouva 34 scolopendres du genre *Scolopendra* (dont 9 *S. morsitans*) et 16 rongeurs (dont 3 *Nannomys* sp.). 19 vipères contenaient des scolopendres, contre 12 qui avaient consommé des rongeurs ; seules 3 d'entre elles avaient consommé l'un et l'autre. Par ailleurs, furent trouvés dans les contenus intestinaux trois restes d'ophidiens (dont un *Psammophis*), un crapaud (*Bufo* sp.), une araignée, un scarabée, trois fourmis, trois arthropodes non identifiés et deux folioles de tamarinier (*Tamarindus indica*). Il n'y avait pas de corrélation entre la taille (ou le sexe) des *Echis* (35 cm en moyenne) et le type de proie. La prédation des rongeurs par les vipéridés est bien connue (Villiers, 1975). Elle favorise la présence de ces ophidiens aux abords des maisons et dans les champs. La consommation de reptiles, de batraciens et d'insectes est également bien établie. En revanche, l'importance de la capture de scolopendres était jusqu'ici, à notre connaissance, complètement ignorée, même si Villiers signale la prédation de myriapodes par des reptiles fouisseurs des genres *Typhlops* et *Leptotyphlops* et que Warrell & Arnett (1976) décrivent une consommation occasionnelle de myriapodes par *Echis*. La capture de *S. morsitans*, lucifuge et hygrophile, commune dans les concessions, pourrait expliquer la fréquence des rencontres homme/serpent la nuit, au crépuscule et à l'aube, dans et autour des habitations, principalement au début et à la fin de la saison des pluies. Le venin du genre *Echis* est essentiellement hémorragipare, très efficace pour la prédation des petits rongeurs. On peut se demander alors dans quelles conditions s'est développée, de manière aussi importante, la prédation des scolopendres. La description récente d'une glande supralabiale à débouché externe dans le genre *Echis* (Ineich & Tellier, 1992), cas unique chez les serpents, apporte peut-être des éléments de réponse. Le développement de cette étude, sur plusieurs cycles pluviométriques, dans d'autres régions d'Afrique soudano-sahélienne (Nigeria notamment), chez d'autres espèces du genre *Echis*, serait riche d'enseignements pour la compréhension du fonctionnement de la biocénose et des interactions entre l'homme et son milieu.

Revault, P., 1996. — *Scolopendra morsitans* Linnaeus, 1758: a characteristic prey of the african carpet viper *Echis ocellatus* Stemmler, 1970. *In*: Geoffroy, J.-J., Mauriès, J.-P. & Nguyen Duy - Jacquemin, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 495-499. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

INTRODUCTION

In the Sudan and the Sahel Savannah, the genus *Echis* (Reptilia, Viperidae) contributes largely to bites of human and serious envenomations (HABIB, 1992; HUGHES, 1976; ROMAN, 1980). In the Ouagadougou area (Burkina Faso, Fig. 1), snake bites occur during the rainy season (Fig. 2), mostly during the night (including dusk and dawn), sometimes in houses, and principally at the beginning and the end of the season. Therefore it seems necessary to look for the factors that determine the encounter between man and snake.

The rainfall pattern and the predation pressure play a leading role in the dynamics and organization of tropical herpetofaunas (BARBAULT, 1991). We were curious to know more about the diet of *Echis ocellatus* in Burkina Faso.

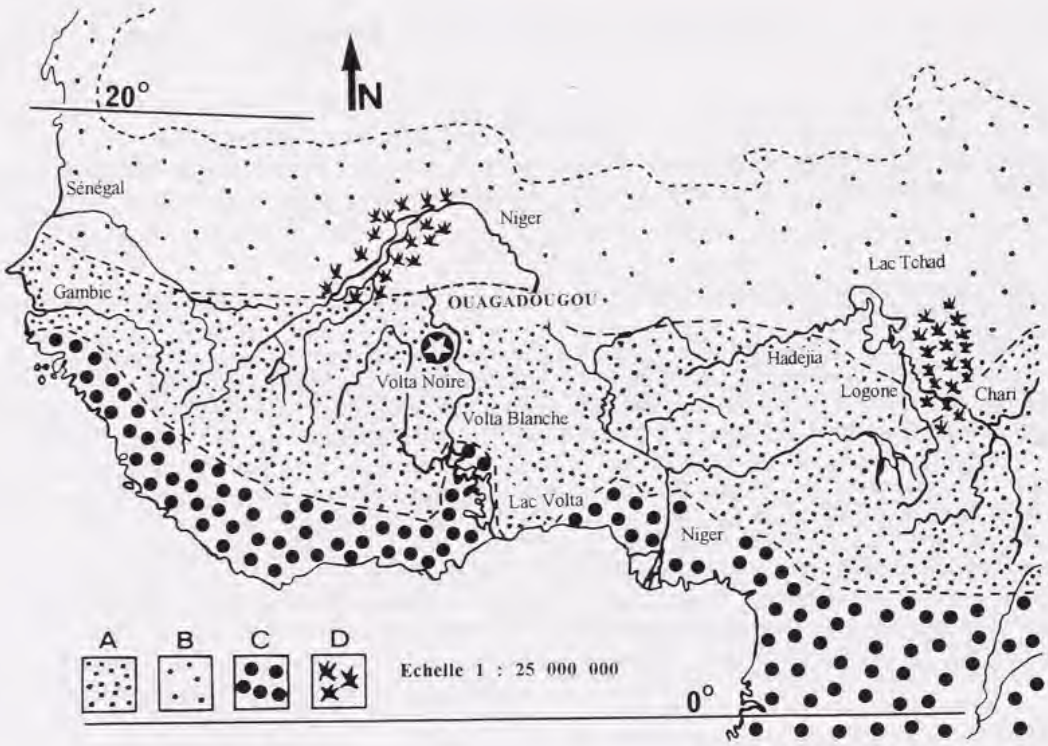


FIG. 1. — Study area in the Sudan Savannah: Ouagadougou (Burkina Faso). A: Sudan savannah, B: Sahelian steppe, C: Tropical forest, D: Marsh areas; according to LACOSTE (1990).

MATERIAL AND METHODS

In October (end of the rainy season) and in April (beginning of the rainy season), a snake collection was carried out, corresponding to the first and last bite peak (Fig. 2).

Echis ocellatus are crepuscular vipers, living especially in the Sudan Savannah (Fig. 1). Peasants captured the vipers from an area 100 km around Ouagadougou as they encountered them. The snakes were preserved in 10% formalin solution, after an injection with formalin (anus, tail). They were dissected in the 15 days after capture. The size, the sex were noted and the digestive content analysed (from the cardia to the anus). The animals were preserved in 60° alcohol (Laboratoire des Reptiles et Amphibiens MNHN, Paris, n° 3110-3117).

Source : MNHN, Paris

RESULTS

47 *Echis ocellatus* were captured (39 in October in three localities: Gonsé, Saponé and Sapogo, and 8 in April in one locality: Kouloulou). The average length of 41 individuals, was 35 cm (2 individuals were 18 and 21 cm, the others were longer than 30 cm). The sex-ratio was ≠ 1. Five animals had non mature eggs (2 in April and 3 in October).

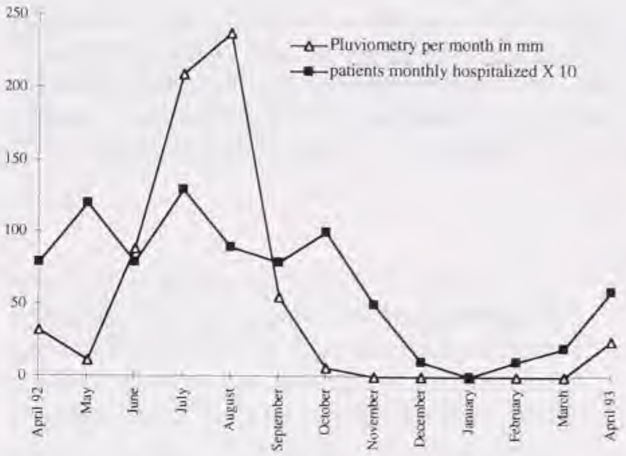


FIG. 2. — Correlation between snake bites and rainfall: number of patients monthly hospitalized at the H. N. of Ouagadougou (n = 83) during one year / Rain fall (665.5 mm in one year) from "Direction de la Météorologie".

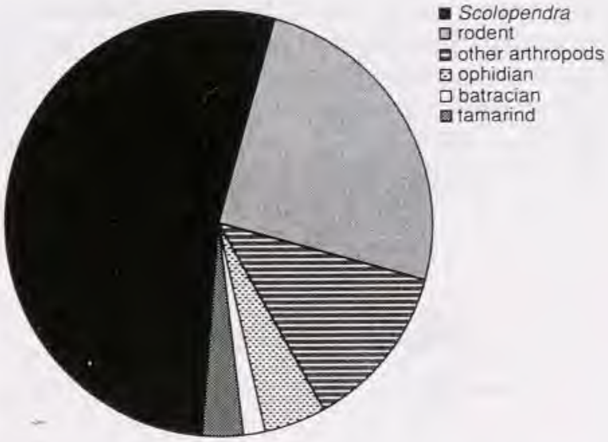


FIG. 3. — Digestive contents of 39 *Echis ocellatus*: taxonomic distribution of the 64 prey-types identified in the gut after dissection. Tamarind = tamarind leaflets).

There was no difference of size (or sex) between the vipers with no digestive content and the others. Equally, there was no correlation between the type of prey and the size (or the sex) of the *Echis*.

8 *Echis* had no gut contents. The gastro-intestinal contents of the 39 others are presented in Figure 3. 34 centipedes, genus *Scolopendra*, were found. 9 were *S. morsitans* (J.-M. DEMANGE *det.*). The average size, amongst 15 individuals, was 8 cm (from 5 to 12 cm). 21 snakes were concerned.

16 rodents were found. 3 belonging to the genus *Nannomys* (M. TRANIER *det.*). The average size, found in 6 individuals, was 8 cm (from 6 to 12 cm). 15 snakes were concerned.

In three cases only, the snake had swallowed a rodent and a *Scolopendra*.

The other prey were: 3 snakes (1 *Psammophis* sp.), 2 tamarind leaflets, 1 Solifugae, 1 Coleoptera, 3 ants and the rest non identifiable arthropods.

Scolopendra is a common prey of vipers (Fig. 4) but does not appear to be inportant in rice fields at Saponé in comparison with the other areas (Sudan Savannah).

DISCUSSION

The centipede *Scolopendra morsitans* is lucifugal and requires moisture. Snakes may enter houses at night, dusk and dawn, looking for centipedes and this may explain the frequency of man-snake encounters.

This study encompassed only one rainy season. Further data are required on the age, predators and reproduction of *Echis ocellatus*.

BARBAULT (1991) doesn't describe such a characteristic diet for *Echis ocellatus*, in the Sudan Savanah (Ivory-Coast) even if WARRELL & ARNETT (1976) describe that *Echis* sp. in Nigeria occasionnally swallow Myriapoda. In the same region, VILLIERS (1975) cites the

Source : MNHN, Paris

predation of Myriapoda by the genus *Typhlops* and *Leptotyphlops*, both burrowing snakes. In South Africa, Colubridae from the genus *Asparallactus* (BROADLEY & COK, 1993) are called centipede eaters, described as having an effective venom, making their prey helpless. But to our knowledge, the selective predation on centipedes amongst Viperidae, and especially on *Scolopendra*, has not been remarked up to now. The venom of *Echis* is essentially haemorrhagiparous, very effective for the predation of small rodents but not for centipedes. It can be asked under what type of conditions did the predation of centipedes develop in such a characteristic way. Is this particular diet found uniquely in the area of Ouagadougou, amongst the genus *Echis*? It is possible that the supra labial gland described by INEICH & TELLIER (1992) may be important in this respect.

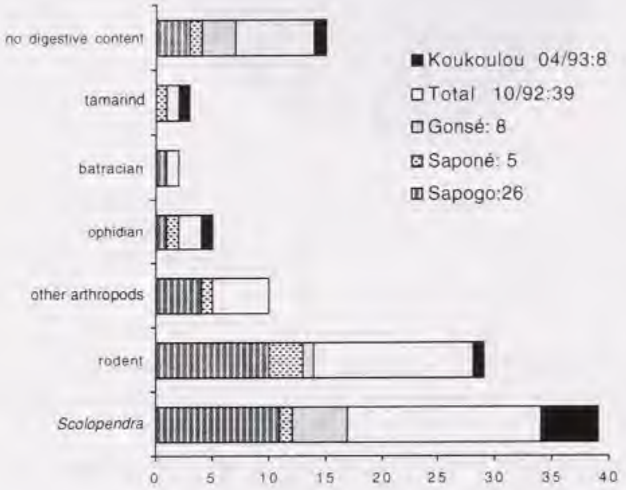


FIG. 4. — Relative importance of prey-types captured by 47 *Echis ocellatus* in 4 snake sampling sites.

LEWIS (1970) has pointed out that *Scolopendra morsitans* is atypical, amongst the scolopendromorph centipedes that have been studied, because it seems to be surface active throughout the year. The life cycle is completed in one year and young individuals appear in March and *again* in October (LEWIS, 1974).

In order to develop this study in the future, observations are required on several seasonal cycles and in other regions of Sudan and Sahel savanna. Other species of Echis should be investigated in order to enrich the comprehension of the biocenosis and the interaction between man and his environment.

ACKNOWLEDGMENTS

I am much indebted to Dr. M. GOYFFON for his assistance in collecting information and to Dr. I. INEICH for his help to conserve and analyse the snake collection.

My thanks are also due to Prof J.-M. DEMANGE for the identification of centipedes, and to Dr. J. C. GAUTUN for his support related to collecting the snakes.

REFERENCES

BARBAULT, R., 1991. — Ecological constraints and community dynamics: linking community patterns to organismal ecology. The case of tropical herpetofaunas. *Acta Œcologica*, **12** : 139-163.

BROADLEY, D. G. & COK, E. V., 1993. — *Snakes of Zimbabwe*. Bundu Series, Zimbabwe, Longman, 152 pp.

HABIB, A. G., 1992. — Tropical snake bite in Northern Nigeria. A clinical review. *Nigerian Medical Practitioner*, **23** : 3-8.

HUGHES, B., 1976. — Notes on African Carpet Viper *Echis carinatus, Echis leucogaster* and *Echis ocellatus* (Viperidae, Serpentes). *Rev. Suisse Zool.*, **83** : 359-371.

INEICH, I. & TELLIER, J. M., 1992. — Une glande supralabiale à débouché externe chez le genre *Echis* (Reptilia, Viperidae), cas unique chez les serpents. *C. R. Acad. Sci. Paris*, **315** : 49-53.

LACOSTE, Y., 1990. — *Atlas 2000. La France et le monde*. Paris, Editions Nathan, 160 pp.

Source : MNHN, Paris

LEWIS, J. G. E., 1970. — The biology of *Scolopendra amazonica* in Nigerian Guinea savannah. *Bull. Mus. natl. Hist. nat.*, **41, suppl. 2** : 85-90.

LEWIS, J. G. E., 1974. — The ecology of Centipedes and Millipedes in Northern Nigeria. *Symp. zool. Soc. Lond.*, **32** : 423-431.

ROMAN, B., 1980. — *Serpents de Haute Volta.* Ouagadougou, Editions du CNRST, 129 pp.

VILLIERS, A., 1975. — *Les serpents de l'Ouest africain.* Initiations et études africaines. N° II, 3ème édition. Dakar, Université de Dakar. IFAN, 195 pp.

WARRELL, D. A. & ARNETT, C., 1976. — The importance of bites by the saw scaled or carpet viper (*Echis carinatus*): Epidemiological studies in Nigeria and a review of the world literature. *Acta Trop., Basel*, **33** : 307-341.

Source : MNHN, Paris

Source : MNHN, Paris

The Life Cycle of *Cylindroiulus latestriatus* (Curtis, 1845)

Karin VOIGTLÄNDER

Staatliches Museum für Naturkunde Görlitz, PF 300 154, D-02806 Görlitz, Germany

ABSTRACT

A population of *Cylindroiulus latestriatus* from Eastern Germany has been studied in 1983. On the basis of the characterization of stadia, by the defence gland method, all possible variations of increments of ring numbers are given and a scheme of developmental pathways is built up. By examining individual development and the resulting main pathways a review of the regularities in the development of ring increment in the species *C. latestriatus* can be made. The increment of body rings together with the increase of body length, volume, and biomass allows to clarify the regulatory mechanisms in the development of julids. The age structure and life cycle of the East German population of *C. latestriatus* is compared with those of other authors, made in different countries and habitats, and with different methods of stadial determination. They are generally in agreement with only minor differences.

RÉSUMÉ

Le cycle de vie de *Cylindroiulus latestriatus* (Curtis, 1845).

Le cycle de vie d'une population de *Cylindroiulus latestriatus* d'Allemagne orientale a été étudiée selon la méthode de comptage des glandes répugnatoires et comparée aux résultats obtenus par d'autres auteurs. Les divers modes d'acquisition de nouveaux anneaux sont explorés et l'hypothèse d'un mécanisme régulateur de l'ontogenèse des julides est testée sur le matériel étudié.

INTRODUCTION

The study of the post-embryonic development and the laws of anamorphosis in millipedes has a high level of interest. Life histories offer phylogenetical information and help to clarify relationships between millepede orders.

Despite there being more problems to overcome than in other groups (e.g. Chordeumatida, Polydesmida) the order Julida is, with 41 species investigated for developmental pathways, one of the most frequently studied orders. Difficulties in investigations arise from the overlap of ring numbers of successive stadia. The total number of rings cannot be used to determine the stadia. Maturity is reached in several different stadia and ages (see ENGHOFF, DOHLE & BLOWER, 1993). For this reason many more investigations on the life cycles of this order are necessary.

The species *C. latestriatus* has been studied very intensively by BLOWER & GABBUTT (1964) and by BIERNAUX (1972). Other authors (COTTON & MILLER, 1974; LANG, 1954) have given additional remarks to the life history of this species. No detailed investigations were known from Germany.

VOIGTLÄNDER, K., 1996. — The life cycle of *Cylindroiulus latestriatus* (Curtis, 1845). *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 501-508. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

This situation offers the rare possibility of comparing the results from different sites and by various methods of stadial determination.

MATERIAL AND METHOD

About 100 specimens of *C. latestriatus* were collected from the litter layer under hazelnut bushes in a garden at a very dry site in NE Germany (Premnitz near Brandenburg) in 1983. A more detailed description of the habitat is given by VOIGTLÄNDER (1987).

Irrespective of stadia and age, the specimens were reared at room temperature in Petri dishes with a natural substrate on a layer of moist filter paper to study the further development.

To identify the stadia of the freshly collected specimens I used the defence gland method (HALKKA, 1958; BROOKES, 1963). Measurements of length and width as well as weighing were made on living specimens (for the methods see VOIGTLÄNDER, 1987).

CHARACTERIZATION OF STADIA AND DEVELOPMENTAL PATHWAYS

The Table 1 shows the total numbers and increments of defence glands related to each moult. The first and by far the biggest variation in increase of rings (or defence glands respectively) occurs at the moult into the fourth stadium. From this there follows a nearly regular decrease both in variation and in newly occuring ring numbers.

TABLE 1. — Total number and increment of defence glands in *C. latestriatus*.

	n	n	increment of defence glands							
stadium	individuals	defence glands	8	7	6	5	4	3	2	1
II	33	1								
↓						100.0				
III	31	6								
↓			6.4	3.2	12.9	51.6	25.8			
IV	30	10-14								
↓				3.3	46.7	43.3	6.7			
V	42	15-19								
↓					40.5	42.9	16.7			
VI	45	19-25								
↓					4.4	66.7	24.4	6.7		
VII	45	24-29								
↓						4.4	28.9	66.7		
VIII	50	28-32								
↓								10.0	88.0	2.0
IX	29	31-34								
↓								6.9	65.5	27.6
X	16	32-36								
↓									12.5	87.5
XI	9	33-38								
↓										100.0
XII	5	34-39								
↓										100.0
XIII	1	38-40								
↓										100.0
XIV	1	40								

Source : MNHN, Paris

On the average, the highest increase in rings is gained during the moult into the Vth stadium. The following moultings show progressively fewer numbers of added rings, down to 1.0 from the XIth stadium on.

The pathways of defence gland increments (Fig. 1) are originally determined by the "basic groups", according to PEITSALMI (1981), occuring at the IVth stadium. Basic groups with the highest and lowest gland numbers become "normalized" during the following 3 moults.

Regarding the number of observed moulting events (indicated by the little numbers in Fig. 1), it is clearly visible that 2 or 3 main pathways of development (thick lines) dominate.

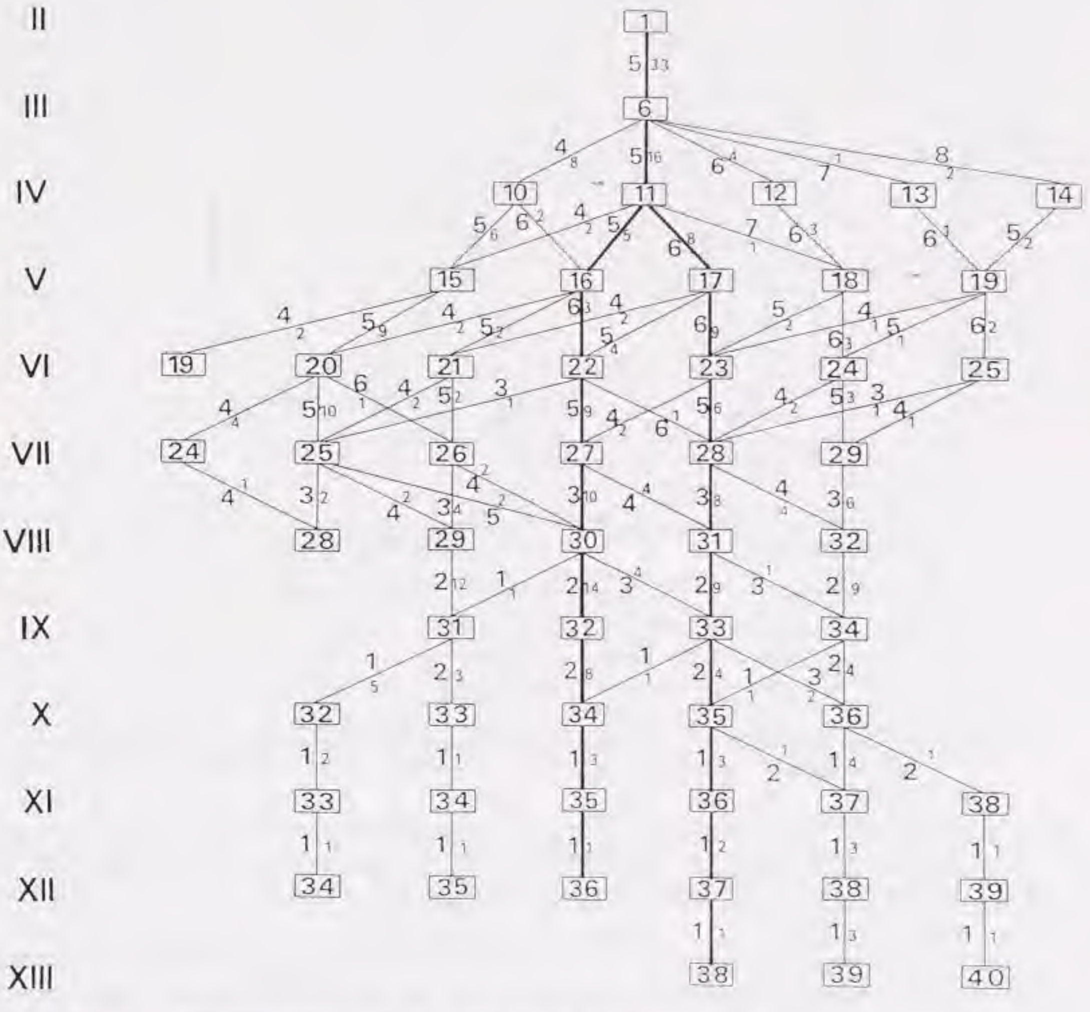


FIG. 1. — Observed defence glands and the main developmental pathways of *C. latestriatus*.

In Figure 2 the post-embryonic development of *C. latestriatus* is shown as a result of studies in an oak wood on sandy soil in England (BLOWER & GABUTT, 1964), in marram dunes on the east coast of Scotland (COTTON & MILLER, 1974), in a field of carrots in Belgium (BIERNAUX, 1972) and in a garden on sandy soil in Germany (this paper). The methods used for estimations were the analysis of discontinuities of dimensions (BLOWER & GABBUTT, 1964), the observation of eye rows (COTTON & MILLER, 1974; BIERNAUX, 1972) and the number of defence gland (BIERNAUX, 1972 and this paper).

Source : MNHN, Paris

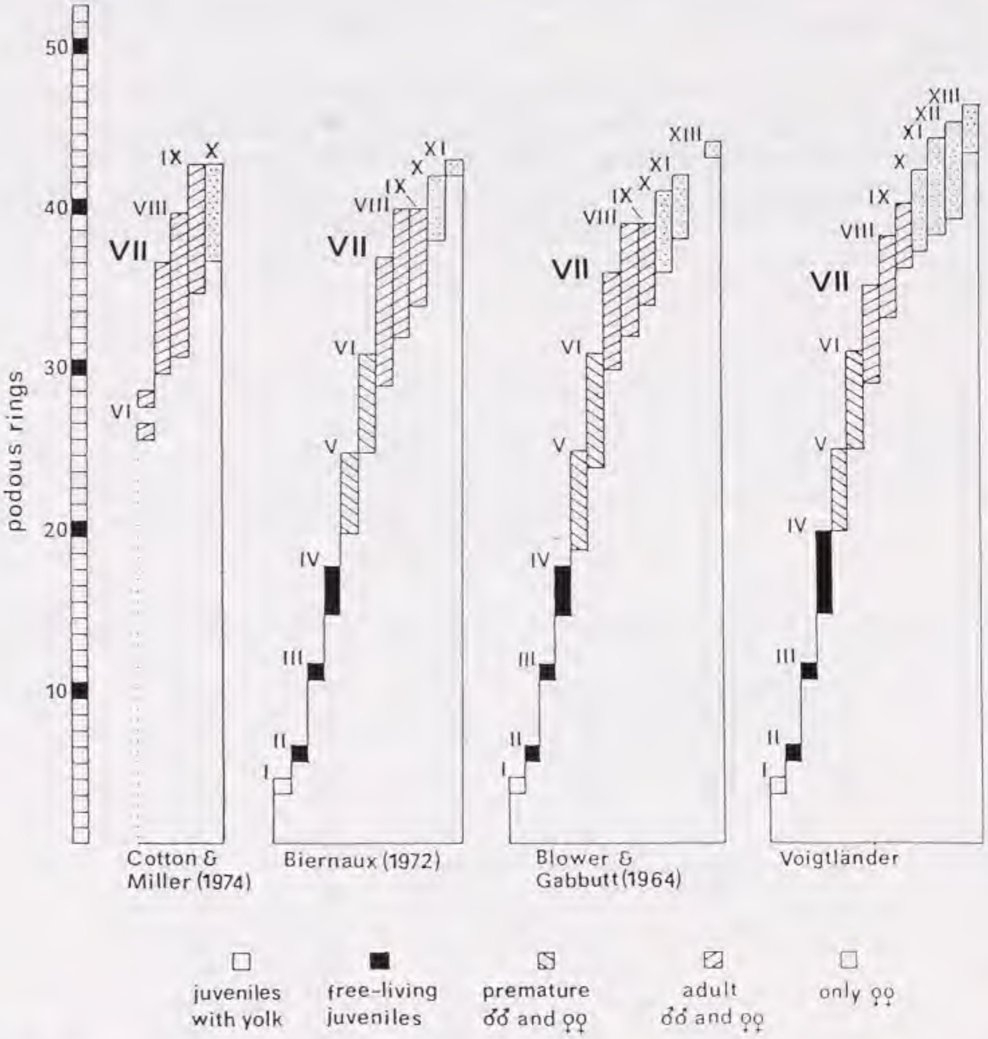


FIG. 2. — The post-embryonic development in *C. latestriatus* studied by different authors. The first stadium to contain mature animals is the stadium VII. Results by VOIGTLÄNDER deal with this paper.

Up to stadium IV there are few differences between the results. Later on variations increase, for example specimens of stadium XI show a maximum of 41 rings according to BLOWER & GABBUTT (1964), 42 rings according to BIERNAUX (1972) and 43 rings after the results of the present study.

Males reach stadium IX only, irrespective of the indicated ring numbers according to all authors. The highest stadium reached by females is stadium XIII, showing 43 rings (BLOWER & GABBUTT, 1964) or 45 rings (this work). COTTON & MILLER (1974) estimate the highest stadium being X with up to 42 podous rings. They argue that some females which were placed in stadia IX and X in their investigation may belong to stadia XI or XII because it is difficult to determine the addition of ocelli to the ocular field at higher stadia.

The results of the investigations of stadial development of *C. latestriatus* correspond with the rules known for other Juliformia. The species belongs to the group of anamorphotic julids with an indefinite number of body ring increments.

As in other related species, such as *Cylindroiulus punctatus* or *Kryphioiulus occultus*, older stadia add one new body ring only at each moulting.

Source : MNHN, Paris

C. latestriatus reaches stadium XIII as a maximum. The low number of stadia seems to be typical for Cylindroiulinae (for example *Enantiulus nanus* XV, *K. occultus* XIV, *C. punctatus* XIV).

GROWTH INCREMENTS

Because of the relatively low number of specimens observed, these results are not significant but they indicate the overall tendency.

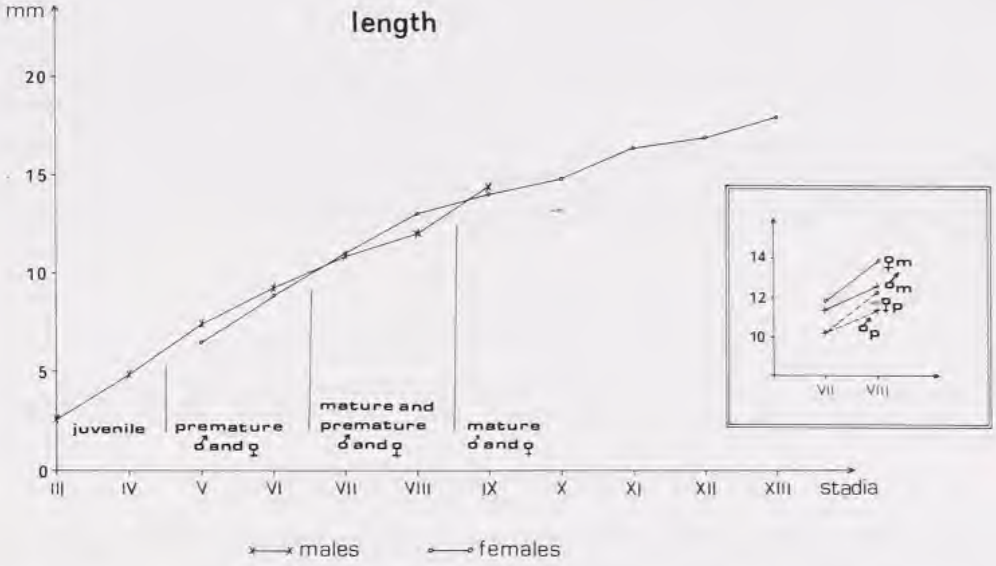


FIG. 3. — Mean increase of length in *C. latestriatus* (p = premature, m = mature individuals).

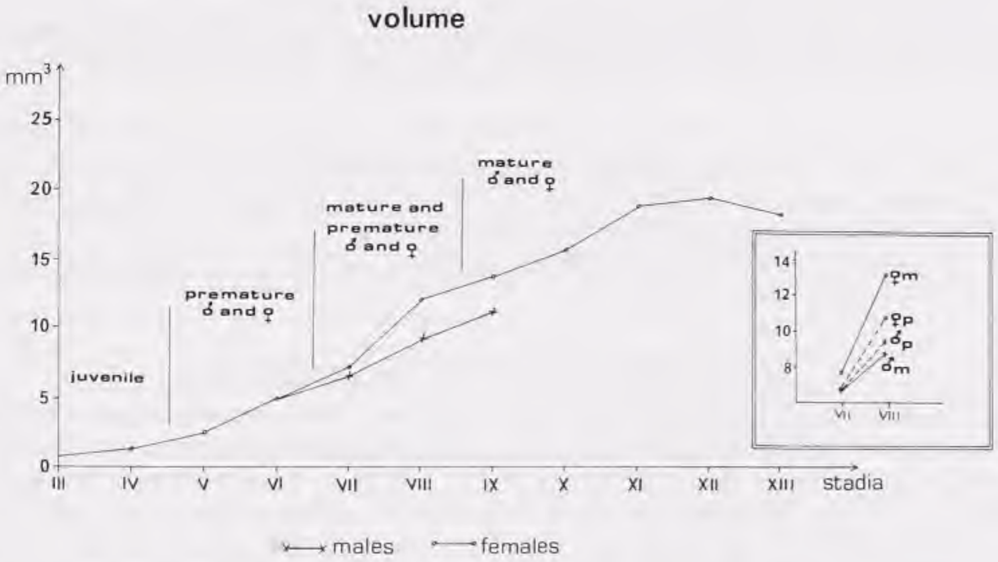


FIG. 4. — Mean increase of volume in *C. latestriatus*.

Source : MNHN, Paris

Each moult of *C. latestriatus* is correlated with a relatively constant increase of length (Fig. 3). The same is true for the volume except for the XIIIth stadium of females (Fig. 4). Judging from the biomass (Fig. 5), more or less identical results can be seen, with the exception of some flattened sections of the curves for gravid females according to the number of eggs. In contrast the numbers of newly formed rings decrease at each moult.

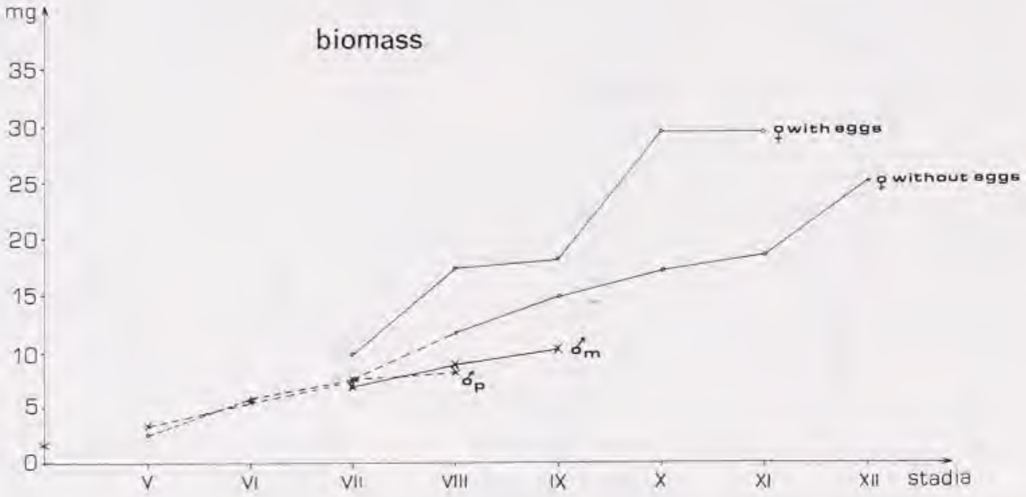


FIG. 5. — Mean increase of biomass of *C. latestriatus*.

ENGHOFF, DOHLE & BLOWER (1993) have suggested 4 hypotheses to explain the range of addition of rings. According to these, the addition can depend on:

1. the available energy ,
2. the randomness of splitting of the germinal field,
3. a combination of 1+2,
4. a predisposition to variable increments for whatever reason.

As to point 1, observations on *C. latestriatus* cannot be explained by different energy supply if we suppose that available energy is not continously decreasing from stadium IV to the end.

Furthermore the growth in biomass is not closely related to the numbers of added rings.

Regarding hypothesis 2 it should be considered that the first 3 stadia have an entirely constant increment, and after that there is a nearly constant decrease of addition from the Vth stage on. These events cannot be explained by randomness.

A predisposition of some kind may be assumed, although the cause has not yet been identified.

EGG LAYING AND EARLIEST DEVELOPMENT

BLOWER & GABBUTT (1964) did not find any eggs neither in the field nor in culture. They assume, that eggs are laid in small numbers and not aggregated together in a typical nest.

In this study one nest was found consisting of 6 eggs in a rearing vessel in the laboratory at the beginning of May. The pupoids "hatched" after two weeks and developed after 4 days into a typical stadium I with 3 pairs of legs. The duration of this stadium was 3 to 4 days. The following stadium II is the first free living and feeding one. All observed young specimens overwintered at stadium V.

Source : MNHN, Paris

SEXUAL DIMORPHISM AND BEGINNING OF MATURITY

The sexes of *C. latestriatus* can be distinguished first at stadium V. Premature males clearly show the absence of the leg pairs on the 7th body ring. Animals with appearance of females need a further moult to clarify the real sex.

In all investigations made in *C. latestriatus* both sexes reached maturity in stadium VII or rarely in VIII. In females the eggs, which can be seen through the body wall, indicate the maturity.

BLOWER & GABBUTT (1964) have investigated precisely the gonopod development of some species. They pointed out, that 2 to 3 gonopod stadia exist in *C. latestriatus*, which extend over 5 developmental stadia of the males. The primary gonopod stage always coincides with the fifth stage, the secondary and also the tertiary with the sixth. Mostly, maturity is reached in stadium VII, rarely the tertiary gonopod stage extends to stadium VIII or IX (1 male). Corresponding with their investigations only 20% premature males in stadium VIII were found here, but no premature specimens in stadium IX.

Females reached the highest stadium of XII in their natural habitat (Table 2) and stadium XIII in the laboratory (only ?). Males reach a maximum of stadium VIII (with the exception of one male in stadium IX). This suggests that males die mostly after one or certainly after two reproduction periods.

TABLE 2. — Moulting activity of *C. latestriatus*.

Month	Febr.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
juvenile + premature	2	1	2	12		12	3	2	2	-	-
mature	-	-	2	5	4	4	10	6	18	3	3
Total	2	1	4	17	4	16	13	8	20	3	3

The temporal distribution of the moults is shown in Table 2. Juveniles, premature and mature individuals are able to moult over the whole year, but with different maxima. Adults mostly moult in autumn, juveniles and prematures in spring and summer. This agrees with other characteristics of the species such as the high locomotory activity of adults in spring during the search for the partners. A moult is the peak of the physiological activity and can only take place after the end of a reproduction period. Young individuals can moult in spring too, because they do not reproduce.

AGE STRUCTURE AND LIFE CYCLE

The age structure of the population is strongly connected with the life cycle of *C. latestriatus*. The population consists of all stadia and age groups throughout the whole year with exception of the youngest stadia, which can only be found after the egg laying period.

As a consequence of the different speeds of the individual development, individuals of several generations can belong to the same stadium. This may firstly be observed in stadium VI with two overlapping generations. In stadium VIII the overlap can include 3 generations. This fact makes the interpretation of samples very difficult. This is the reason why a combination between field observations and results of laboratory rearings was necessary.

The egg laying takes place in spring. The young individuals develop, according to the results of all authors, into the stadia (III), mostly IV or V (and VI) in which they overwinter. Individuals of stadium VI may belong to the first generation or to the second if they started from overwintered stadium III. Provided that the maturity moult takes place in autumn

Source : MNHN, Paris

(VOIGTLÄNDER, 1987) it is concluded, that the first reproduction is possible at the 2nd or 3rd year of life. This short time for development is very uncommon for julids.

Males die after one or at least two reproduction periods. They live for a maximum of 3 or 4 years, as a rule only 2-3 years. Females have on average a higher expectation of life usually 3-4 years, with a maximum of 7-8 years.

REFERENCES

BIERNAUX, J., 1972. — Chorologie et étude biologique comparée de deux familles de Myriapodes - Diplopodes belges: les Blaniulidae et les Iulidae. Dissertation, Gembloux, Faculté des Sciences agronomiques de l'Etat, 193 pp.

BLOWER, J. G., & GABBUTT, P. D., 1964. — Studies on the millipedes of a Devon oak wood. *Proc. zool. Soc. London,* **143** : 143-176.

BROOKES, C. H., 1963. — Some aspects of the life histories and ecology of *Proteroiulus fuscus* (Am Stein) and *Isobates varicornis* (Koch) (Diplopoda) with information on other blaniulid millipedes. Thesis, Univ. Manchester.

COTTON, M. J., & MILLER, P. F., 1974. — A population of *Cylindroiulus latestriatus* (Curtis) on sand dunes. *Symp. Zool. Soc. Lond.,* **32** : 589-602.

ENGHOFF, H., DOHLE W. & BLOWER, J. G., 1993. — Anamorphosis in Millipedes (Diplopoda) - The present state of knowledge with some developmental and phylogenetic considerations. *Zool. J. Linnean Soc.,* **109**: 103-234.

HALKKA, R., 1958. — Life history of *Schizophyllum sabulosum* (L.) (Diplopoda, Julidae). *Ann. Zool. Soc., Zool. bot. Fenn. "Vanamo",* **19** : 1-72.

LANG, J., 1954. — Postembryonalentwicklung der Diplopoden. *Vest. Cs. spol. zool. (Acta soc. zool. Bohemoslov.),* **18** : 161-176.

PEITSALMI, M., 1981. — Population structure and seasonal changes in activity of *Proteroiulus fuscus* (Am Stein) (Diplopoda, Blaniulidae). *Acta Zoologica Fennica,* **161**: 1-66.

VOIGTLÄNDER, K., 1987. — Untersuchungen zur Bionomie von *Enantiulus nanus* (Latzel, 1884) und *Allajulus occultus* C. L. Koch, 1847 (Diplopoda, Julidae). *Abh. Ber. Naturkundemus. Görlitz,* **60** : 1-116.

Source : MNHN, Paris

Life-Cycle of the Millipede *Melogona voigti* (Verhoeff, 1899) from a Suburban Forest in South Bohemia

Karel TAJOVSKY

Institute of Soil Biology, Academy of Sciences of the Czech Republic
370 05 Ceske Budejovice, Czech Republic

ABSTRACT

A population of the millipede *Melogona voigti* in a suburban deciduous forest in South Bohemia has been studied by soil sampling. The changes of density in the course of the year and the post-embryonic development have been described. The biological cycle was annual for the greatest part of the population. The effects of climatic factors on the life-cycle of Chordeumatida are discussed.

RÉSUMÉ

Cycle de vie du diplopode *Melogona voigti* (Verhoeff, 1899) dans une forêt suburbaine décidue du sud de la Bohème.

Une population de *Melogona voigti* d'une forêt décidue suburbaine du sud de la Bohème a été étudiée par échantillonnage du sol. Les variations de densité au cours de l'année et le développement post-embryonnaire sont décrits. Le cycle est annuel pour la plus grande partie de la population. Les effets des facteurs climatiques sur le cycle des chordeumatides sont discutés.

INTRODUCTION

Three species of the genus *Melogona* Cook, 1895 (= *Microchordeuma* Verhoeff, 1896) are distributed in Central and North-West Europe. Post-embryonic development of *M. scutellare* (Ribaut, 1913) was described by BLOWER (1978, 1979) and that of *M. gallica* (Latzel, 1884) by DAVID (1984). Some primary data for the third species *M. voigti* (Verhoeff, 1899) were published by VERHOEFF (1913, 1928) and later supplemented by SCHUBART (1957) and by DUNGER & STEINMETZGER (1981). *M. scutellare*, belonging to the subgenus *Chordeumella* Verhoeff, 1897, has eight post-embryonic stadia and adults with 28 body segments. *M. gallica* and *M. voigti* belong to the subgenus *Melogona* Cook, 1895, the adults of which have 30 body segments and mature one stadium later.

During the faunistic research in South Bohemia, a suburban forest near Ceske Budejovice was discovered to contain a population of *Melogona voigti*. To obtain data for completion of its life-cycle, soil sampling was used.

TAJOVSKY, K., 1996. — Life-cycle of the millipede *Melogona voigti* (Verhoeff, 1899) from a suburban forest in South Bohemia. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 509-514. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

STUDY SITE AND METHODS

The population of *Melogona voigti* was studied in the suburban deciduous forest Stromovka in south-west outskirts of Ceske Budejovice-city in South Bohemia (Czech Republic). Stromovka (430 m a.s.l., average air temperature 7.8°C, precipitation 620 mm, see Fig. 2) is an allochtonous sparse wood dominated by *Populus nigra* L. and *Alnus glutinosa* (L.) Gaertn. The plant cover consists mostly of *Urtica dioica* L. and *Filipendula ulmaria* (L.) Max. The site is characterized by brown soil type (gleic cambisol) with mull-moder to mull humus horizon, pH (H_2O) 4.4.

Ten soil samples (sampling area 1/16 m2, depth 5 cm) were taken at approximately fortnightly intervals from February 24, 1992 until April 19, 1993. Millipedes were heat extracted from soil samples by modified Kempson extraction apparatus (KEMPSON *et al.*, 1963). For the evaluation of post-embryonic development of *M. voigti*, the numbers of body segments, pairs of legs and ocelli were counted. Females were dissected and the presence or absence of eggs investigated.

RESULTS

Population density and dynamics during the year

Sequential fortnightly sampling confirmed, that the millipede *M. voigti* is active during the whole year. Mean annual density of the population under study was 60.6 ind.m2. During the winter months up to March, adults only were present (Fig. 1). The first increase in density in mid-April can be connected with the increasing activity of adults. Practically all successive peaks of density were due to culminations of separate post-embryonic stadia: 11.5. - stadium III, 26.5. - stadium IV, 13.7. - stadia V and VI, 24.8. - stadium VII, and 4.11. - stadium IX (new adults). The marked depression in mid-June was probably due to the rainfall deficiency and the consequent drying up of the litter and upper soil layer. The maximum number of adults was observed in November. In winter months the density of millipedes decreased.

Mating and oviposition

Both, mating and oviposition appeared to take place early in spring, judging from the appearance of stadium II as from the first half of April. In the field the mating was observed still in April. Dissection of females showed the presence of eggs in the ovarium from November until the end of April. Therefore it was not possible to be more precise about the time of oviposition or the number of eggs laid.

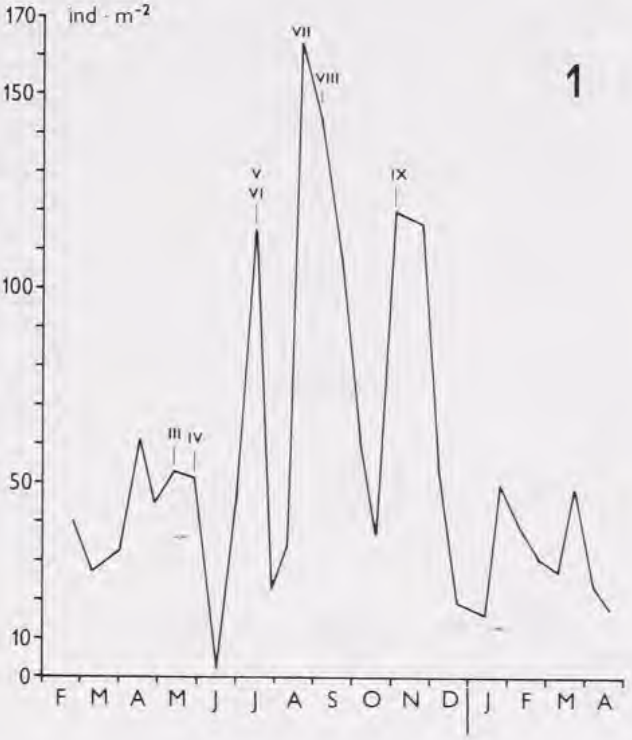
Post-embryonic stadia

Numbers of body segments (podous and apodous) and numbers of pairs of legs for individual stadia of *M. voigti* are given in Table 1. *M. voigti* has nine post-embryonic stadia. Sexual differentiation is in the last three stadia. Numbers of ocelli and their arrangement in the ocular field based on the material from South Bohemia are given in Figure 3.

TABLE 1. — Post-embryonic stadia of *Melogona voigti*. Pleurotergites - number of podous rings, apodous rings and telson, Ad = adults, F = female, M =male.

Stadium:	I	II	III	IV	V	VI	VII	VIII	IX(Ad)
pleurotergites:	6	8	11	15	19	23	26	28	30
podous:	4	5	7	10	14	18	22	25	27
apodous:	1	2	3	4	4	4	3	2	2
leg pairs:	3	5	10	16	24	32	40	46	49(F)
	"	"	"	"	"	"	39	44	45(M)

Source : MNHN, Paris



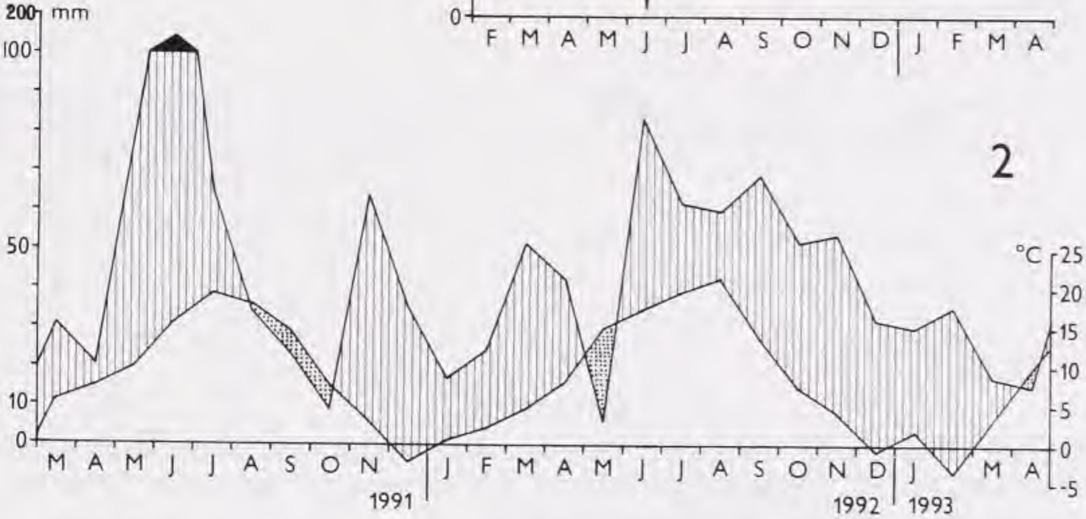


FIG. 1. — Density of dynamics of the millipede *M. voigti* showing the separate post-embryonic stadia.
FIG. 2. — Mean monthly temperature and monthly precipitations for Ceské Budejovice.

Post-embryonic development

The adults were present until the end of May (Figs 4 and 5). The first stadium was not recorded by the method used. Individuals of stadium II were noted in mid-April. Stadium III was observed from the end of April until the end of May with a maximum in the first half of May. Stadium IV appeared as from the end of May in the highest density, then it was present during the whole of June through to mid-July, and was also noted at the end of August. Stadium V was present in soil samples from the end of June until the end of August, stadium VI from mid-July up to September 21. Both stadia VII and VIII observed from the end of July and mid-August, respectively, were present up to the beginning of October. At that time the first adults (stadium IX) appeared. The absence of stadia VII and VIII in mid-October and following samples confirmed the end of post-embryonic development.

Source : MNHN, Paris

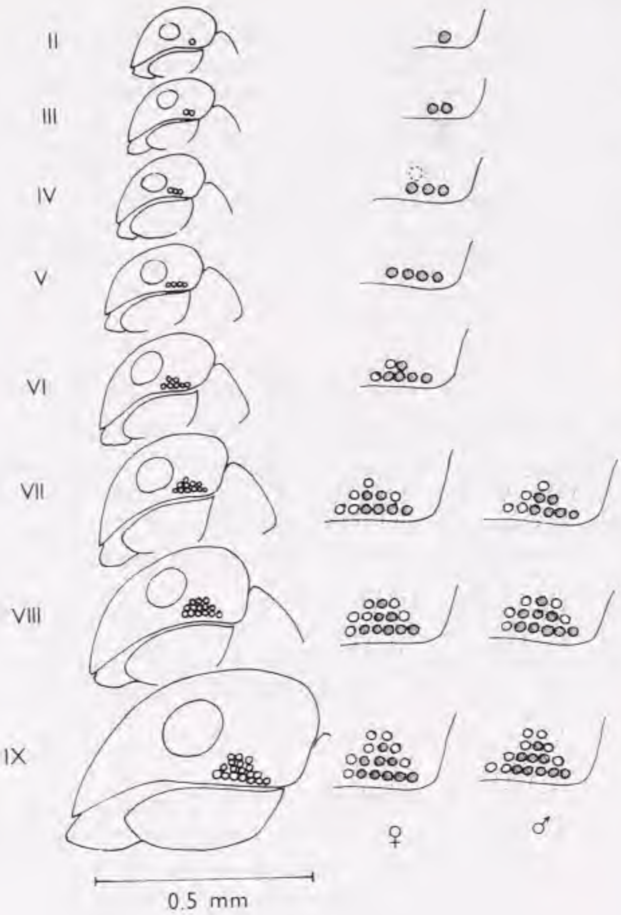


FIG. 3. — Growth of the ocular field from stadium II to maturity. Ocelli invariably present are cross-hatched, ocelli not always present are open, the rows of ocelli are marked.

In the period March 30 - July 13, in addition to beside stadia II to VI, the individuals of stadia VI, VII and VIII were also present. This means that a smaller part of the previous year's population did not quite complete its development and overwintered in the same locality as stadia VI and/or VII and VIII. The successive sampling did not quite elucidate, whether this part of the population finished their development during this second year. During the next March and April 1993, the younger overwintering stadia VI, VII and VIII were not sampled.

M. voigti is therefore largely an annual millipede, however a part of the population can take more than one year to complete its life-cycle.

DISCUSSION

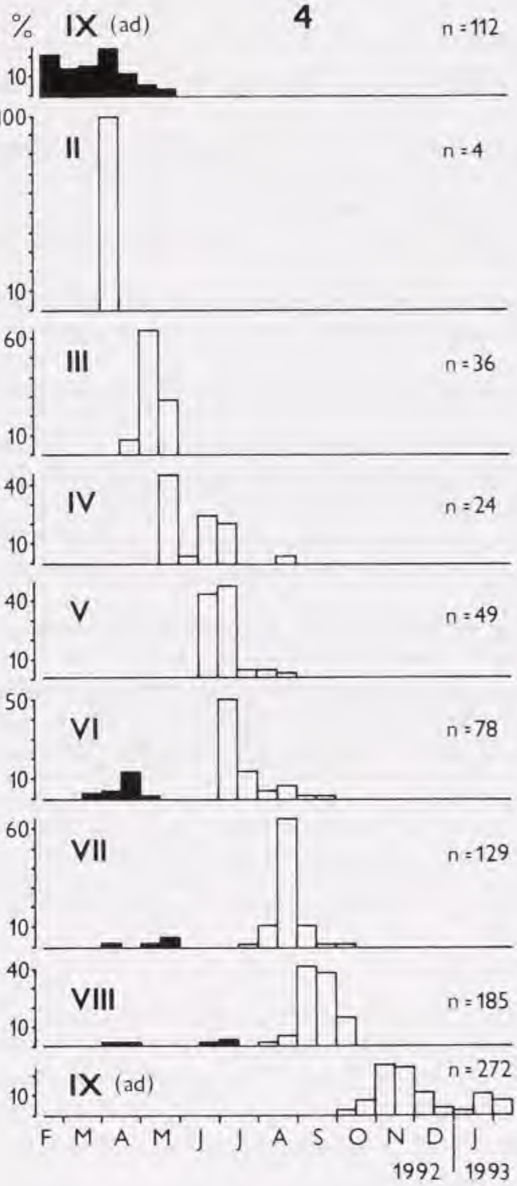
Numbers of body segments and numbers of pairs of legs for individual stadia of *M. voigti* correspond to the general pattern for the suborder Chordeumatidea (BLOWER, 1984) and are in agreement with the data for *M. gallica* (DAVID, 1984).

VERHOEFF (1913, 1928) described the occurrence of the adult millipedes of *M. voigti* from October until May and of the juveniles in the remaining part of the year. SCHUBART (1957) confirmed these data, and DUNGER & STEINMETZGER (1981) found the adults even in mid-June. In contrast to VERHOEFFs' data (VERHOEFF, 1928), the appearances of individual stadia III to VII were always later and the development up to stadium IX was shorter (Fig. 5). In this way, post-embryonic development of *M. voigti* differs from that of the related West-European species *M. gallica* (Fig. 5). A shorter period of development with a fast sequence of older stadia V-VIII of the population under study may be the result of the colder continental climate.

The influence of climatic factors on life-cycles of Chordeumatida is known. In addition to prolongation of the time to maturity, longevity and a general slowing down of the life-cycle with the increase in altitude and decrease in temperature (MEYER, 1990), there is evidence of the interruption of the life-cycle in a part of the population due to the unfavorable microclimatic conditions (dryness, coldness) and of the life-cycle prolongation into the following year (PEDROLI-CHRISTEN, 1978; DAVID, 1989). The prolongation of life-cycle and the suggestion of

Source : MNHN, Paris

a two year development for *M. gallica* were described for a French population (DAVID, 1984) and noted for a British population as well (BLOWER, 1984). DAVID (1984) mentioned that this phenomenon can be either regular, i.e. a certain smaller part of the population always hibernates as a juvenile stadium (in our case stadia VI, VII and/or VIII) to finish the development during the next year, or this phenomenon is evoked under certain conditions. On the other hand *M. scutellare*, probably also due to the shorter post-embryonic development with eight stadia, is only an annual species (Fig. 5).



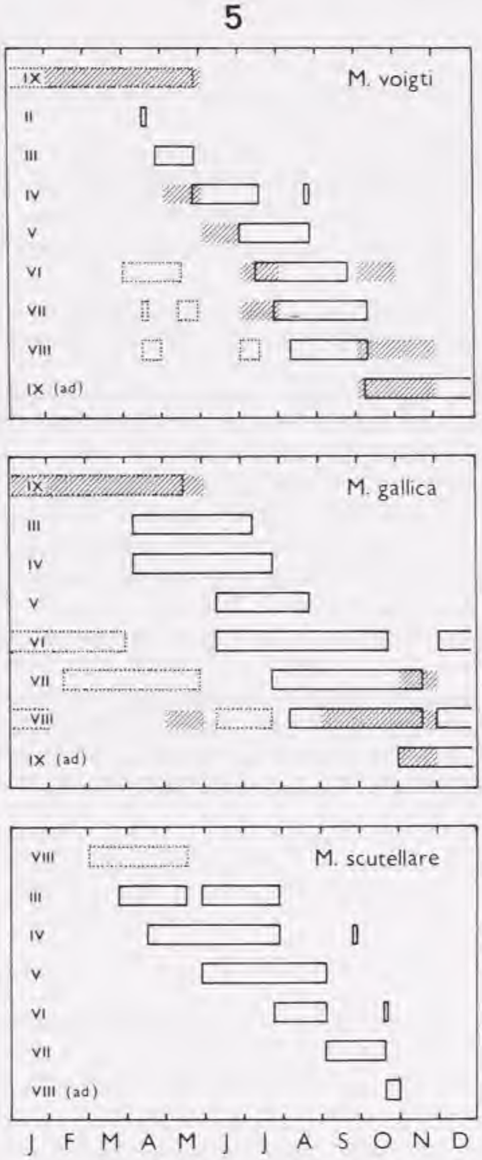


FIG. 4. — Post-embryonic development of *M. voigti* during the year. Filled fields: generation of previous year 1991.
FIG. 5. — Comparison of the life-cycles of *M. voigti*, *M. gallica* (according to DAVID, 1984), and *M. scutellare* (according to BLOWER, 1979). Areas with dotted borders - generation of previous year, cross-hatched areas - according to VERHOEFF (1928).

Source : MNHN, Paris

In 1991 a severe rainfall deficiency between August and October was observed (Fig. 2). At this time stadia VI, VII and VIII of *M. voigti* were present, which were then found again the next spring 1992. These stadia were probably minimally active and/or quite inactive in winter, because only adults were sampled. No convincing evidence about the development of this stadium VIII into stadium IX was given by subsequent sampling. Either the members of this stadium mature together with the new generation of stadium VIII or, only a small part of them mature which is difficult to find by sampling, or they do not mature at all. Consequently the absence of juvenile stadia VI, VII and/or VIII in spring 1993 is associated with favorable climatic conditions during the year 1992, when the whole population probably completed its development.

REFERENCES

BLOWER, J. G., 1978. — Anamorphosis in the Nematophora. *Abh. Verh. naturwiss. Ver. Hamburg, (NF)*, **21/22** : 97-103.

BLOWER, J. G., 1979. — The millipede faunas of two British limestone woods. *In* : M. CAMATINI, *Myriapod Biology*. London, Academic Press : 295-306.

BLOWER, J. G., 1984. — The British Chordeumatidae. *Bull. Br. Myriapod Group*, **2** : 8-23.

DAVID, J. F., 1984. — Le cycle annuel du Diplopode *Microchordeuma gallica* (Latzel, 1884). *Bull. Soc. zool. Fr.*, **109** : 61 - 70.

DAVID, J. F., 1989. — Le cycle biologique de *Chamaesoma brolemanni* Ribaut & Verhoeff, 1913 (Diplopoda, Craspedosomatida) en forêt d'Orléans (France). *Bull. Mus. natl. Hist. nat., Paris, 4e sér., 11, section A*, **3** : 639-647.

DUNGER, W. & STEINMETZGER, K., 1981. — Ökologische Untersuchungen an Diplopoden einer Rasen-Wald-Catena im Thüringen Kalkgebiet. *Zool. Jb. Syst.*, **108** : 519-553.

KEMPSON, D., LLOYD, M., GHELARDI, R., 1963. — A new extractor for woodland litter. *Pedobiologia*, **3** : 1-21.

MEYER, E., 1990. — Altitute-related changes of life histories of Chordeumatida in the Central Alps (Tyrol, Austria). *In* : A. MINELLI, *Proceedings 7th Intern. Congr. Myriapodology*. Leiden, E. J. Brill : 311-322.

PEDROLI-CHRISTEN, A., 1978. — Contribution à la connaissance du développement post-embryonnaire de *Craspedosoma alemannicum* Verhoeff et de *Xylophageuma zschokkei* Bigler (Diplopoda, Nematophora) dans une tourbière du Haut-Jura Suisse. *Rev. suisse Zool.*, **85** : 673-679.

SCHUBART O., 1957. — Die Diplopoden der Mark Brandenburg. Eine Õkologische Studie. *Mitt. Zool. Mus. Berlin*, **33** : 3-94.

VERHOEFF K. W., 1913. — Erscheinungszeiten und Erscheinungsweisen der reifen Tausendfüssler Mitteleuropas und zur Kenntnis der Gattungen *Orobainosoma* und *Oxydactylon*. *Verh. Zool.-Bot. Ges. Wien*, **63** : 334-381.

VERHOEFF, K. W., 1928. — Diplopoda 1. *In* : H. G. BRONN's *Klassen und Ordnungen des Tierreichs*, **5**, Leipzig, Akademische Verlagsgesellschaft : 1-1072.

Source : MNHN, Paris

Life Cycles and Reproductive Strategies in Local Populations of *Rossiulus kessleri* (Lohmander) (Julidae, Diplopoda) from Isolated Habitats

Bella R. STRIGANOVA

Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia

ABSTRACT

Peculiarities of the postembryonic development and reproductive parameters in separate populations of *Rossiulus kessleri* Lohmander, 1926 were studied in two remote isolated forest habitats in the dry steppes of South Russia. Observations were carried out in a natural river-plain forest and shelter forest plantation differing in the edaphic and hydrothermal conditions. Seasonal rhythms of the development, duration of different stages, age and stage of the first reproduction in females, fecundity and natural mortality were considered in both populations. Patterns of the life-cycle of *Rossiulus kessleri* in secondary dry anthropogenic habitats seem to determine the following features of the reproductive strategy: delay in first reproduction and decrease of a total egg-production, which is compensated by low mortality rates in adult stages. Population differences in *Rossiulus kessleri* from isolated habitats are discussed in terms of K-selection and expansion capacity.

RÉSUMÉ

Comparaison des cycles de vie et des stratégies de reproduction de populations locales de *Rossiulus kessleri* (Lohmander) (Julidae, Diplopoda) dans des habitats isolés.

Les modalités du développement post-embryonnaire et de la reproduction de populations séparées de *Rossiulus kessleri* Lohmander, ont été étudiées dans deux habitats forestiers isolés des steppes sèches du sud de la Russie. Les observations ont été effectuées dans une forêt naturelle de plaine et dans une plantation forestière protégée différant par leurs conditions édaphiques et hydrothermiques. Les rythmes saisonniers du développement, la durée des différents stades, l'âge et le stade de la maturation sexuelle des femelles, la fécondité et la mortalité naturelle ont été pris en compte dans les deux populations. Les modalités du cycle de vie de *Rossiulus kessleri* dans des habitats secs anthropisés semblent déterminer les paramètres des stratégies de reproduction - retard de la première reproduction et diminution de taille des pontes - qui sont compensés par un faible taux de mortalité des adultes. Les différences entre populations d'habitats isolés sont discutées en terme de sélection-K et d'augmentation de la capacité biotique.

INTRODUCTION

Reproductive parameters and peculiarities of the postembryonic development have been studied in a number of diplopod species. These indices indicate variation in separate species and in separate populations of the same species from different geographical regions. For example, inter-population differences in the number of sexual and epimorphic stages of males have been recorded in *Bacillozonium nodulosum, Narceus annularis, Spelaeoglomeris doderoi* (SAHLI,

STRIGANOVA, B. R., 1996. — Life cycles and reproductive strategies in local populations of *Rossiulus kessleri* (Lohmander) (Julidae, Diplopoda) from isolated habitats. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 515-522. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

1974). In different populations of *Schizophyllum sabulosum* the number of asexual stages during anamorphic development was found to vary from 3 to 5 (HALKKA, 1958; SAHLI, 1968, 1969). Interpopulation differences seem to be especially strongly expressed in species with polyzonal ranges, inhabiting sites with various edaphic and hydrothermic conditions.

The aim of this work was to compare the life-cycles and the reproductive indices in local isolated populations of *Rossiulus kessleri* from a river floodplain forest and shelter forest strips in the dry steppe subzone of Southern Russia.

Rossiulus kessleri is abundant in the forest-steppe and steppe zones of the European part of Russia. It usually predominates in diplopod communities of both natural and anthropogenic habitats (STRIGANOVA, 1977). These diplopods are well adapted to the climatic conditions of a steppe landscape with a hot and dry summer season. *Rossiulus kessleri* is often located in plots with tree and bush cover. Numerous aggregations of this species occured in ravine and river plain forests and in wind protecting forest plantations (PRISHUTOVA, 1985; SIZOVA, 1985; STRIGANOVA, 1972; STRIGANOVA & PRISHUTOVA, 1990).

Extensive ploughed fields with a long-term monoculture of wheat are characteristic of this region of Russia. Plots with the natural tree and bush cover preserved and artificial forest strips represent isolated island habitats. The natural exchange between these forest islands seems to be impossible for non-flying invertebrates. The perennial isolation of separate populations of diplopods in island habitats suggests the possibility of the existence of different microevolutionary trends in populations living in diverse ecological situations.

SITES AND METHODS

Materials for this study were collected in Rostov and Stavropol regions in two sites being 30-40 km apart:

1. River flood-plain forest of one of the Don tributaries two species dominated: *Salix alba, Alnus glutinosa.* Soil was grey sandy river-plain soil. Litter layer was a constant, 7-10 cm depth, grass cover under a closed tree canopy.

2. 30-year old shelter forest strip in a watershed position. Predominate tree species: *Fraxinus excelsior, Robinia pseudoacacia, Populus nigra.* Soil - typical chernozem of the loamy texture. Litter layer was 23 cm depth, completely decomposed by June. Grasses covered about 70 % of the ground under the canopy.

The habitats differed significantly in the hydrothermic regime of the upper soil horizons. Soil humidity in the river-plain forest was conststantly high, due to the high level of ground water. A high relative humidity at aboveground level was maintained by a dense grass cover. Dry leaf litter dried out only in mid-summer during a drought.

The forest plantation was situated in the zone of an unstable moisture. The litter and soil dried out in summer and the relative humidity of the upper horizon ranged between 5-12 %.

Quantitative samples of diplopods were taken twice per month in both plots from April to October. Diplopods were collected by a hand-sorting from standard quadrats (25 x 25 cm, depth 10 cm).

The live body mass, sex and developmental stage were determined in all specimens sampled. Mature females were dissected to record the presence of eggs.

Periods of the spring moulting, oviposition, presence of juveniles and start of the winter diapause were recorded. The post-embryonic development (longevity of separate stages, growth of the body mass and mortality) was studied in the laboratory.

Eggs obtained from females kept into laboratory jars were placed in Petri dishes. Both longitudinal and transversal diameters of eggs were measured to compare egg sizes from different populations. Larvae that hatched from eggs in the laboratory were reared in groups in jars with soil and leaf litter taken from their natural habitats.

RESULTS

The spring moult of *Rossiulus kessleri* in the river-plain was observed in late April. Diplopods moulted in the soil and did not build moulting chambers. Oviposition was completed in May, and in the mid-June pupoids were recorded in experimental clutches.

In the forest plantation the spring moulting was delayed by 10-15 days. Almost the diplopods built moulting chambers what was observed in both the natural habitat and laboratory). Females began to oviposit in late June, and young larvae appeared in July-August. During dry years the oviposition was delayed until autumn.

Source : MNHN, Paris

The stadium of 1st oviposition differed in separate populations: X - in the river-plain and XI - in the forest plantation. Relative numbers of egg-laying females increased in progressively older stadia (Fig. 1). The percentage of egg-laying females increased in stages X-XII in the river-plain from 56 to 100%. In the forest plantation the percentage of egg-laying females was much lower in all reproductive stages and increased from 19% to 81%.

Mature females showed differences in body mass and fecundity (Figs 2, 3). An increase in the fecundity of older stadia has been recorded in other diplopod species - *Cylindroiulus latestriatus, C. punctatus, Julus scandinavius* (BAKER, 1978; BLOWER, 1970). The relationship between body mass and fecundity has been described in *Ommatoiulus moreleti, Julus scandinavius* and *Glomeris marginata* (HEATH, BOCOCK & MOUNTFORD, 1974). The multiple correlation between the developmental stage, body mass and fecundity has been calculated for both populations of *R. kessleri* under study(PRISHUTOVA & MINORANSKY, 1984). The correlation coefficients averaged 0.91 - for the river-plain and 0.80 - for the forest plantation. Figure 3 shows that the smaller females of the stage XII from the river-plain have a higher fecundity than bigger females of the same stage from the forest plantation.

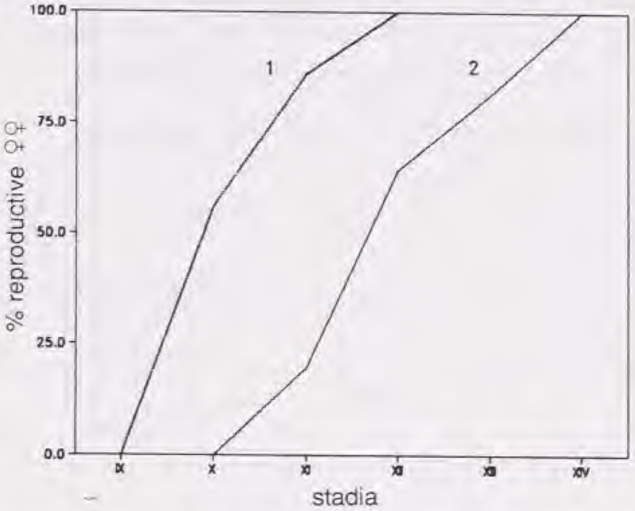


FIG. 1. — Relative number of reproductive females (%) in the older stadia of the development. 1: river-plain forest (n=98); 2: wind protecting forest plantation (n=113).

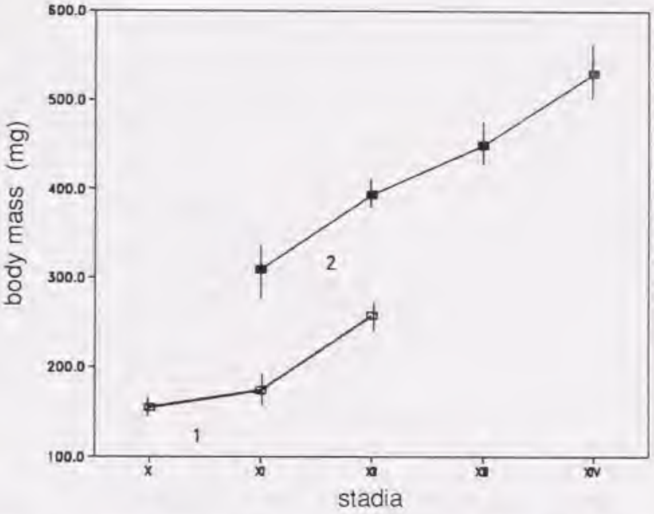


FIG. 2. — Body mass of mature females (mg) in the older stadia of the development. The bars represent one standart error of the mean. 1: river-plain forest (n=98); 2: wind protecting forest plantation (n=113).

TABLE 1. — Total volume (mkl) of the egg production in females of different stages from separate populations of *R. kessleri*.

Stadia	X	XI	XII	XIII	XIV
River-plain forest	34.969	37.587	58.157		
Forest plantation	-	61.446	67.683	76.923	104.874

Source : MNHN, Paris

Egg sizes had clear interpopulation differences: river-plain: longitudinal diameter (mm) 0.826 ± 0.03 and transversal diameter (mm) 0.658 ± 0.03; forest plantation: longitudinal diameter (mm) 0.860 ± 0.03 and transversal diameter (mm) 0.714 ± 0.01 (P = 0.001) (PRISHUTOVA, 1985). The mean egg volumes were calculated approximating their form to an ellipsoid. Individual mean volume of eggs from the river-plain averaged 0.187 mkl and that from the forest plantation 0.231 mkl. Table 1 shows the total volume of egg production in females of different stages from both populations.

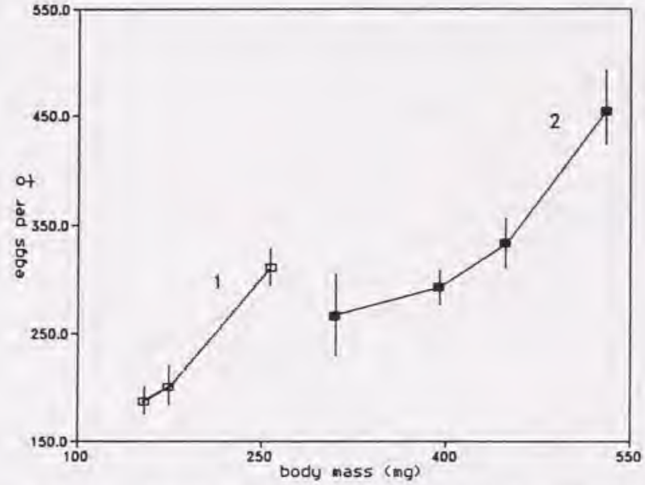


FIG. 3. — Fecundity vs. body mass in mature females. $\overline{x}$±SE. 1 & 2 as in Figure 1.

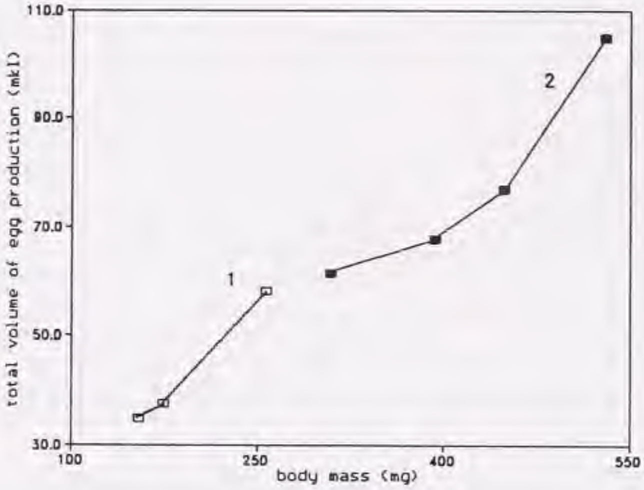


FIG. 4. — Relationship between the mean body mass of reproductive females and the total volume of their egg production. 1 & 2 as in Figure 1.

The relationship between the mean mass of reproductive females and the total volume of their egg-production is shown by Figure 4. Correlation coefficients between these indices averaged 0.99 and 0.94 for the population from the river-plain and forest plantation respectively. The correlation for the whole range of female biomass values was not found to be significant.

Duration of individual stadia was different for each population. Figure 5. shows the rates of the development for stadia II-VII in the laboratory. The total duration of these stages averaged 115 days in the river-plain population and 100 days in the forest plantation one. Significant differences (P≤0.05) were observed in stadium VII only, and these were apparently related to differences in sex differentiation. Sex differentiation begins in stadium VII in the river-plain population, and stadium VIII in the forest plantation population.

Rates of post-embryonic development under favourable laboratory conditions were evidently higher than in natural habitats, as revealed by parallel field samples. But the growth of body mass progressed slowly. Mass of individual diplopods in natural habitats was 1.5-2 times as high as that in laboratory specimens of the same stadia.

In the river plain, *R. kessleri* reached V-VIII during the first summer, IX-X the next year, and the 1st reproduction took place during the third year. Individuals of stadium XIV were recorded in this population. The minimum duration of the life-span is 4-5 years.

A mass emergence of young larvae in the forest plantation was observed in August. All larvae built moulting chambers near the soil surface. 10-15 individuals were found in one

Source : MNHN, Paris

chamber. Before a winter diapause they reached III-IV, in the second year - VIII-IX and in the third - X-XI. The first reproduction took place in the fourth year of life. This population had 15 post-embryonic stages. The total life-span is 5-6 years - a year longer than that in the river-plain. During unfavourable years, the number of egg-laying females remained relatively low and did not exceed 40% of the total amount laid by mature females. This seems to be the reason why the life-span of this population can be prolonged to 8 years.

The mortality dynamics were studied under laboratory conditions (Fig. 6). In the river-plain, maximum mortality rates were recorded in adult stages, which reproduced at least once. In the forest plantation a significant increase in natural mortality was observed during the sexual differentiation. These features, together with the differences of seasonal rhythms affect the population structure.

Figure 7 presents the population structure in both habitats during two subsequent years as stadia recorded from soil samples. The bulk of the population in the river-plain was represented by reproductive stadia. The relative importance of the stadium IX increased in autumn because of the recruitment from the younger generation. In different seasons all stadia were present in the population. The seasonal changes in the age composition in both years were similar.

In the forest plantation the pre-reproductive stadium X predominated in the first spring. Older mature were absent. In autumn, stages XI-XII predominated and single specimens of older stadia appeared. The following spring all adult stadia were present, but VIII-X together barely exceeded 10%. Their mass increased slightly by the following autumn. Replacement rates of generations were delayed by a year in the forest plantation, in comparison with those in the river-plain population.

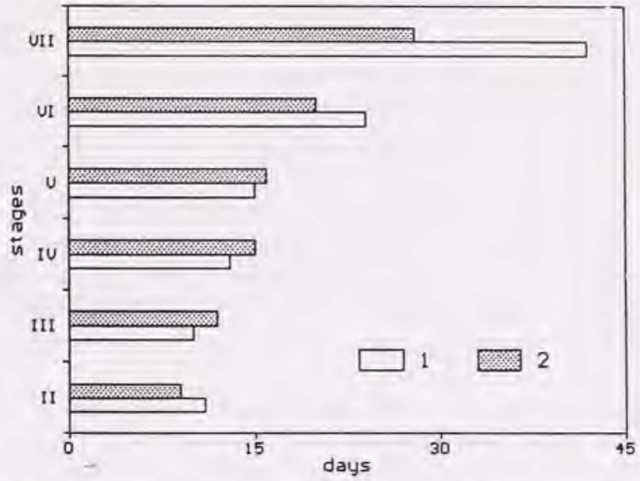


FIG. 5. — Development rates of stadia II-VII in the laboratory for individuals of the river-plain population (1) and of the forest plantation population (2).

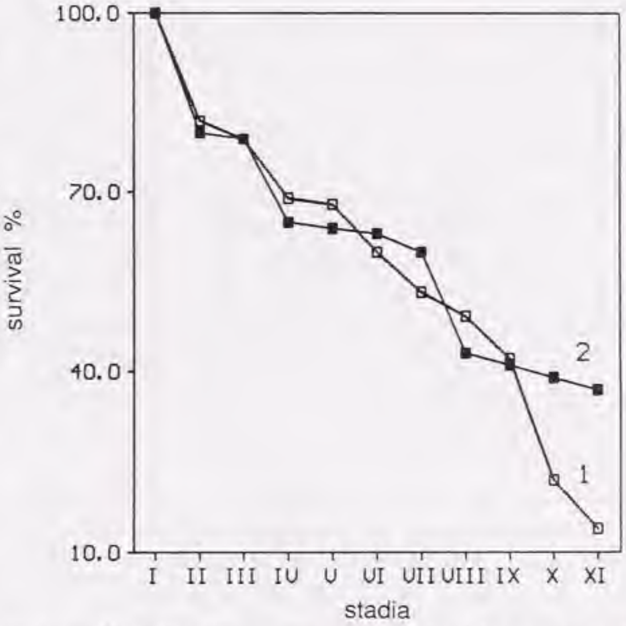


FIG. 6. — Mortality dynamics studied under laboratory conditions for individuals of the river-plain population (1) and of the forest plantation population (2).

Source : MNHN, Paris

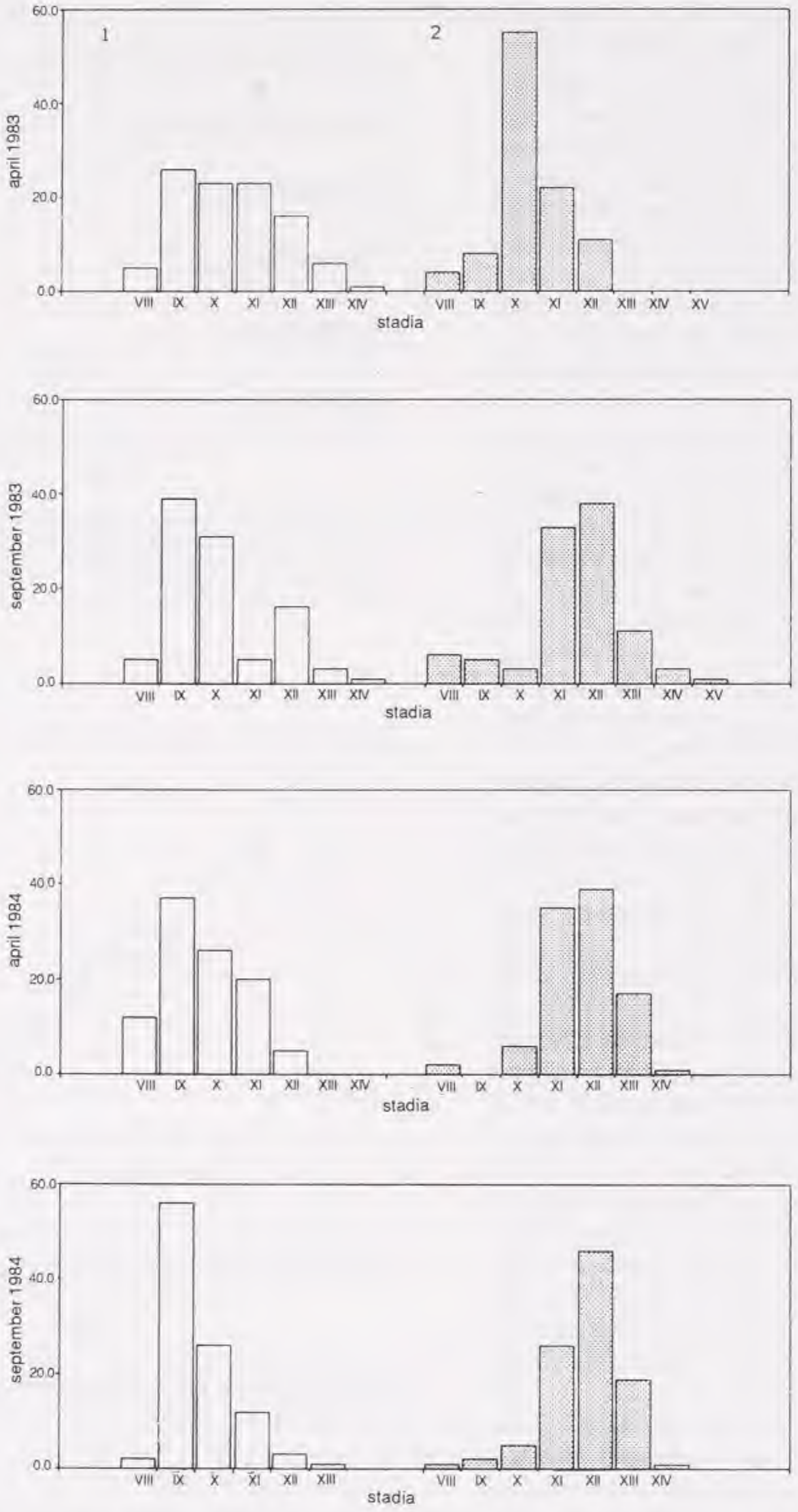


FIG. 7. — Population structure during two subsequent years: river-plain population (1); forest plantation population (2).

Source : MNHN, Paris

DISCUSSION

The analysis of the population structure, the reproduction tactics and the development rates of *R. kessleri* in isolated habitats revealed clear interpopulation differences in the life-cycle. A long summer drought in the soil of an artificial forest plantation promotes a long aestivation period for all stadia. The timing and duration of the summer pause was found to depend on weather conditions in distinct years. The juvenile were particularly susceptible to the hydrothermic conditions. They ceased to feed at the elevated soil temperature even under high moisture levels, while adults continued the normal feeding activity (STRIGANOVA, 1972).

Diplopods living in dried out habitats have to accumulate energy reserves for a summer aestivation, which minimizes the energy quota for reproduction. Accumulation of energy reserves results in the increase in body mass in all stadia, which was observed in diplopods from the forest plantation, in comparison with those from the river-plain (PRISHUTOVA, 1985). The delay in first reproduction can be also interpreted in terms of the energy allocation within the population.

In addition, diplopods from the forest plantation have significant energy expenses for the building of moulting chambers. This building activity was recorded in all stadia. The activity of larvae of the first stadia seems to be provided by a nutrient supply in the eggs. The eggs in these populations were bigger than those from the river-plain populations.

Numerous julid species use to present typical K-selection features such as perennial life-cycle, iteroparity, fixed seasonal rhythms, large body mass etc. (cf. PIANKA, 1970). All these features are characteristics of *Rossiulus kessleri.*

Rossiulus kessleri has 7 asexual stadia. This is the maximum number recorded in Julidae (SAHLI, 1969, 1974). Interpopulation differences in the duration of separate larval stages are insignificant, depending more on the longevity of inactive periods, than on those of an active growth.

The number of sexual stadia shows the inter-population differences (2 - in the river plain and 3 - in the forest plantation). The same was shown in separate populations of *C. teutonicus* (SAHLI, 1969).

Discussion of the factors determining the time of first reproduction considers two alternatives - genetic determination of an age or of a stadium of first reproduction (DAVID, 1992). The results here are consistent with the idea of the stadia as the main determinant. Under unfavorable conditions, for example during heat deficiency, diplopods reach their genetically fixed stadium of maturity at an older age, as described in high mountains (MEYER, 1985).

Interpopulation differences in the stadium of first reproduction can be considered as a result of the micro-evolutionary processes. Populations of *R. kessleri* under study differed in both stage and age of the first reproduction. Age can vary between individuals within the same population, for example in the forest plantation only 18% of females reaching stadium XI participated in reproduction. Hence, age appears to be a more resilient population feature, depending on local conditions.

An acceleration of maturation is associated with a restriction of life-span, as shown, for example, in *Nemasoma varicorne* (BROOKES, 1974). Populations of *R. kessleri* showed the same relationship. The shorter life-span was characteristic of diplopods from the more favourable natural habitat (river plain forest), which can be considered the primary biotope for *R. kessleri* in steppes. The artificial forest plantations represented the secondary habitats populated by these diplopods. The prolongation of the life-cycle and the delay in first reproduction seem to be adaptations to unfavourable anthropogenic habitats.

The prolongation of the life-span to account for long inactive periods is characteristic of many poikilotherms under extreme conditions. K-selection features allow diplopods to select these tactics. The development of this evolutionary trend was recorded only in stable populations capable of increasing their accumulated reproduction reserve with aging, and of continuing an

Source : MNHN, Paris

active growth between reproductive cycles (STEARNS, 1976). These traits are characteristic of *R. kessleri*. This is why this species is so widely distributed in dry steppes where it occurs in both natural and anthropogenic habitats. Life-cycle traits are obligatory population features, they were recorded under both field and laboratory conditions and can be considered as phenotypical features.

REFERENCES

BAKER, G. H., 1978. — The post-embryonic development and life-history of the millipede *Ommatoiulus morelettii* (Diplopoda, Julidae) introduced in south-eastern Australia. *J. zool. London*, **186** : 209-228.

BLOWER, J. G., 1970. — The millipedes of Cheshire wood. *J. zool. London*, **160** : 455-496.

BROOKES, C. H., 1974. — The life-cycle of *Proteroiulus fuscus* (Am Stein) and *Isobates varicornis* (Koch) with notes of the anamorphosis of Blaniulidae. *Symp. Zool. Soc. London*, **32** : 485-501.

DAVID, J. F., 1992. — Some questions about the evolution of life-history traits in Diplopoda. *Ber. nat-med. Verein Innsbruck*, **Suppl. 10** : 143-152.

HALKKA, R., 1958. — Life-history of *Schizophyllum sabulosum* (L.), Diplopoda, Julidae. *Ann. Zool. Soc. Zoologicae Botanicae Fenn.*, **19**, 1-72

HEATH, G. W., BOCOCK, K. L. & MOUNTFORD, M. D., 1974. — The life-history of the millipede *Glomeris marginata* (Villers) in North-West England. *Symp. Zool. Soc. London*, **32** : 433-461.

MEYER, E., 1985. — Distribution, activity, life-history and standing crop of Julidae (Diplopoda, Myriapoda) in the Central High Alps (Tyrol, Austria). *Holarctic Ecology*, **8** : 141-150.

PIANKA, E. R., 1970. — On r- and K-selection. *Am. Nat.*, **104.** : 592-598.

PRISHUTOVA, Z. G., 1985. — Ecology of diplopods in southern steppes (on example of *Rossiulus kessleri* Lohmander). Ph D Thesis, Moscow, Moscow State Pedagogical Institute, 21 pp. (in Russian).

PRISHUTOVA, Z. G. & MINORANSKY, V. A., 1984. — About the reproduction of diplopods *Sarmatiulus kessleri* Lohm. in Nizhny-Don region. *Abstracts All-Union Congress the USSR Entomol. Soc., Kiev*, **2** : 114 (in Russian).

SAHLI, F., 1968. — Observations sur la biologie et la périodomorphose chez le Diplopode *Schizophyllum sabulosum* (L.) en Allemagne. *Bull. Sci. Bourgogne* , **25** : 333-346.

SAHLI, F., 1969. — Contribution à l'étude du développement post-embryonnaire des Diplopodes Julides. *Ann. Univ. saraviensis Reihe math.-naturw. Fak.*, **7** : 1-154.

SAHLI, F., 1974. — Sur les périodes larvaires asexuée et sexuée mâle et sur l'apparition des mâles adultes chez les diplopodes Chilognathes. *Bull. Soc. zool. Fr.*, **99** : 295-305.

SIZOVA, M. G., 1985. — Population structure of diplopods *Rossiulus kessleri* Lohmander in different habitats of Rostov region. *Abstracts IX Intern Colloq. Soil Zool.*, Vilnius : 264.

STEARNS, S. C., 1976. — Life-history tactics: a review of ideas. *Quart. Rev. Biol.*, **51** : 3-47.

STRIGANOVA, B. R., 1972. — Effects of temperature on the feeding activity of *Sarmatiulus kessleri* (Diplopoda). *Oikos*, **23** : 197-199.

STRIGANOVA, B. R., 1977. — Adaptations of diplopods to the life in soils with different hydrothermic conditions. *In* : M. S. GHILAROV, *Adaptation of soil animals to environmental conditions*. Moscow, Nauka : 151-166. (in Russian, English Summary)

STRIGANOVA, B. R. & PRISHUTOVA, Z. G., 1990. — Food requirements of diplopods in the dry steppe subzone of the USSR. *Pedobiologia*, **34** : 37-41.

Source : MNHN, Paris

Survival Strategy of the Terricolous Millipede *Cutervodesmus adisi* Golovatch (Fuhrmannodesmidae, Polydesmida) in a Blackwater Inundation Forest of Central Amazonia (Brazil) in Response to the Flood Pulse

Joachim ADIS*, *Sergei I.* GOLOVATCH ** & *Susanne* HAMANN *

* Max-Planck-Institute for Limnology, Tropical Ecology Working Group, Postfach 165, D-24302 Plön, Germany, in cooperation with National Institute for Amazonian Research (INPA), C.P. 478, 69011-970 Manaus/AM, Brazil

** Institute of Evolutionary Morphology and Ecology of Animals, Russian Academy of Sciences, 33 Leninsky prospect, 117071 Moscow V-71, Russia

ABSTRACT

Reaction of *Cutervodesmus adisi* Golovatch, 1992 to 5-7 months of flooding was studied in 1976/77 and 1983/84 in a blackwater inundation forest near Manaus, Brazil. The study area was annually covered by several metres of floodwater, due to the monomodal flood pulse of the Rio Negro. Juvenile migratory stages with 18 (and 17) segments spent the inundation period on tree trunks. In 1976/77, they represented 42% of all Polydesmida caught in arboreal traps on 6 tree trunks over a period of 18 months (n = 5661). After flooding, the migratory stages of *C. adisi* recolonized the forest floor. They developed to adults which subsequently reproduced. Vertical distribution of 94% of all animals extracted from 0-14 cm soil depth was restricted to the upper 7 cm. Migratory stages of the offspring moved into tree trunks. Trunk ascents began several weeks before forest inundation and after the rainy season had started. Trunk ascents and descents, as well as the vertical distribution of *C. adisi* in the soil during the non-inundation period, are discussed with respect to abiotic factors in the study area (precipitation, insolation, temperature and humidity of soil and air) as well as macroclimatic influences (El Niño events). *C. adisi* is considered to be an endemic species of the blackwater inundation forests in the Rio Negro Valley. Vertical migration of its juvenile stages represents an ethological adaptation to escape annual long-term flooding, which was not found in Polydesmida of neighbouring non-flooded upland forests.

RÉSUMÉ

Stratégie de survie du diplopode terricole *Cutervodesmus adisi* Golovatch (Fuhrmannodesmidae, Polydesmida) dans une forêt inondable de l'Amazonie centrale en réponse à la fréquence des inondations.

Les réactions de *Cutervodesmus adisi* Golovatch, 1992 à une période de 5 à 7 mois d'inondation ont été étudiées en 1976/77 et 1983/84 dans une forêt inondable d'eau noire près de Manaus au Brésil. Le site d'étude est annuellement recouvert par plusieurs mètres d'eau, consécutivemement au flux d'inondation monomodal du Rio Negro. Les stades juvéniles migrateurs à 18 (et 17) anneaux passent la période d'inondation dans les troncs d'arbres. En 1976/77, ils

---

ADIS, J., GOLOVATCH, S. I. & HAMANN, S., 1996. — Survival strategy of the terricolous millipede *Cutervodesmus adisi* Golovatch (Fuhrmannodesmidae, Polydesmida) in a blackwater inundation forest of Central Amazonia (Brazil) in response to the flood pulse. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 523-532. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

représentaient 42% de tous les Polydesmida capturés dans les pièges arboricoles relevés sur six troncs d'arbres durant 18 mois (n = 5661). Après l'inondation, les stades migrateurs de *C. adisi* ont recolonisé le sol forestier. Ils se sont développés en adultes qui se sont ensuite reproduits. La répartition verticale de 94% de tous les individus extraits d'une épaisseur de sol de 14 cm se réduit aux 7 cm supérieurs. Les stades migrateurs issus du recrutement annuel se déplacent sur les troncs d'arbres. L'ascension du tronc commence plusieurs semaines avant l'inondation de la forêt et après le démarrage de la saison des pluies. L'ascension et la descente le long des troncs, de même que la répartition verticale de *C. adisi* dans le sol en dehors de la période d'inondation, sont discutées en rapport avec les facteurs abiotiques du site d'étude (précipitation, insolation, température, humidité de l'air et du sol) ainsi qu'avec les influences macroclimatiques (évènements dûs au El Niño). *C. adisi* est considéré comme une espèce endémique des forêts inondables de la vallée du Rio Negro. La migration verticale de ses stades juvéniles représente une adaptation éthologique lui permettant d'échapper à une inondation à long terme, comportement qu'on ne retrouve pas chez les polydesmides des forêts non-inondées plus élevées.

INTRODUCTION

Terrestrial invertebrates in periodically flooded ecosystems require special "survival strategies" (cf. ADIS, 1992a). In Central Amazonia, the monomodal "flood pulse" (JUNK *et al.*, 1989) of the Rio Negro and the Rio Solimões-Amazon causes flooding of forests near rivers - the so-called seasonal inundation forests (PRANCE, 1979) - and their adjacent shores by several metres of floodwater for 5-7 months each year. Terrestrial invertebrates have adapted to this ecosystem. The fauna comprises terricolous and arboricolous animals. Both groups include non-migrants and migrants. Migratory reaction of terricolous animals is horizontal (following the high water line), vertical (temporal ascent to trunk or canopy) or includes a temporal flight to upland forests. Non-migrants have active or dormant stages under water. The latter pass inundation in naturally available retreats, in self-made retreats or as eggs. Non-migrant arboricolous animals reproduce and live exclusively in the trunk and canopy region, whereas migrants include life stages that live on the ground as well. Characteristics and examples of species for each of these categories are given by ADIS (1992a, b).

In the vicinity of Manaus, millipedes alone display a good variety of responses to seasonal floods. Thus, *Gonographis adisi* Hoffman, 1985 (Pyrgodesmidae, Polydesmida) appears to be unique in being the only hitherto known millipede capable of surviving submersion for up to 11 months due to a hydrophobic secretion layer on the cuticula which enables plastron respiration (HOFFMAN, 1985; ADIS, 1986; MESSNER & ADIS, 1988). On the contrary the even more widespread synanthropic *Muyudesmus obliteratus* Kraus, 1960 (Pyrgodesmidae), another forest floor-dweller, escapes flooding by moving to the non-inundated tree trunks and canopy areas (like most other millipedes); its plastron is incomplete thus long-term submersion is fatal (ADIS, 1986; MESSNER & ADIS, 1988). *Mestosoma hylaeicum* Jeekel, 1963 (Paradoxosomatidae, Polydesmida) generally displays the same pattern of behaviour, with all the phases of its life-history neatly corresponding to local seasonality (ADIS, 1992c). Probably the same holds true for *Prostemmiulus adisi* Mauriès, 1984 (Stemmiulidae, Stemmiulida), perhaps the only one of three congeners (the others being *P. amazonicus* Mauriès, 1984, and *P. wellingtoni* Mauriès, 1984) encountered in inundation forests that shows similar seasonal vertical migrations from the forest floor to the trunk/canopy areas and back (MAURIÈS, 1984). The same can obviously be said about *Moojenodesmus pumilus* Schubart, 1944, *M. susannae* Golovatch, 1992 (Fuhrmannodesmidae, Polydesmida) (GOLOVATCH, 1992a) and *Onciurosoma adisi* Golovatch, 1992 (Paradoxosomatidae) (GOLOVATCH, 1992b).

Another different survival strategy is demonstrated by *Epinannolene arborea* Hoffman, 1984 (Pseudonannolenidae, Spirostreptida), obviously a strict arboricole (HOFFMAN, 1984; ADIS, 1984) which remains in the upper trunk and canopy region unless forced down the trunk by insolation/drought when it retreats under the bark and estivates there.

In this paper, adaptive reaction of the diplopod *Cutervodesmus adisi* Golovatch, 1992 from a seasonal blackwater inundation forest in the Rio Negro valley to the annual flooding is

Source : MNHN, Paris

discussed. Its survival strategy is compared with that of Diplopoda already known to inhabit inundation forests in the surroundings of Manaus.

STUDY AREA AND METHODS

Diplopoda were collected between 1975 and 1988 in the course of ecological studies on terrestrial invertebrates from Central Amazonian floodplains, in particular the seasonal inundation forests (cf. ADIS, 1981, 1984, 1992 a-c; ADIS & SCHUBART, 1984).

The study site was situated on the lower course of the Rio Tarumã Mirím (03°02'S, 60°17'W), a tributary of the Rio Negro, about 20 km upstream from Manaus. The seasonal blackwater inundation forest (for definition see PRANCE, 1979) was situated on a slope and extended from the non-inundated dryland area (= upland or terra firme) with a constant decline (< 5%) to the bare sandy shoreline of the Rio Tarumã Mirím (see profile in BECK, 1976). The central part of the study site was covered annually by up to 3.35 m of floodwater between March/April and August/September. Further information on the study site is given by ADIS (1981, 1984, 1992a), MEYER (1991) and WORBES (1986).

The activity density of Diplopoda evaluated in this study was monitored on the forest floor with 8 ground photo-eclectors of FUNKE (= emergence traps) during the non-inundation period in 1976/77. Trunk ascents and descents were detected at weekly or bi-weekly intervals with arboreal photo-eclectors (= funnel traps) on three tree trunks each of the dominant tree species (cf. Table 1) between December 1975 and May 1977. The killing/preserving agent used in all traps was aqueous picric acid solution (without detergent), which is known to be mostly neutral in terms of attraction or repellence in temperate zones (ADIS, 1979). All capture devices are fully described by ADIS (1981) and FUNKE (1971), who also explain their mode of utilization and function. Trunk ascents of Diplopoda and their activity on the ground were additionally monitored with funnel traps on one tree and with 1-4 emergence traps on the forest floor during the non-inundation periods in 1982/83 and 1983/84, respectively.

Distribution of Diplopoda in the non-flooded soil was studied between September, 1981 and February, 1982. Once a month, six soil samples were taken at random along a transect with a split corer (= steel cylinder with lateral hinges; diameter 21 cm, length 33 cm) which was driven into the soil by a mallet. Each sample of 14 cm depth was then subdivided into four subsamples of 3.5 cm each. Animals were extracted from subsamples following a modified method of KEMPSON (ADIS, 1987).

The presence of Diplopoda in the flooded soil was studied at the end of each inundation period in 1984-88. Twelve soil samples were taken at 3-weekly intervals under water as described above. Each of the subsamples was kept moist for 10-14 days on a grid inside a bucket, which was covered by a cotton screen (sealed up by a plastic snap ring) and contained aqueous picric acid in the bottom. Animals were subsequently extracted with the modified KEMPSON apparatus.

The presence of Diplopoda in tree crowns was tested by fogging canopies with pyrethrum in the early dry season (July 1977, 1979), when the inundation forest was completely flooded (cf. ADIS *et al.* 1984; ERWIN, 1983). Bromeliads, 5-25 m above ground, were also sampled and checked for terrestrial invertebrates in August, 1979 (forest not flooded) and June, 1981 (forest flooded).

Seasonal inundation forests in Central Amazonia are subject to a rainy season (December - May: average precipitation 1550 mm), and a "dry" season (June - November: average precipitation 550 mm, but each month has some rain events; cf. RIBEIRO & ADIS, 1984). Vertical distribution of Diplopoda in relation to changing conditions of soil moisture content, temperature and pH, was statistically evaluated with the linear correlation test (CAVALLI-SFORZA, 1972), using the original field data. This method was also used to evaluate the activity of Diplopoda on the soil surface and tree trunks in relation to insolation, precipitation, temperature and humidity of the air.

The taxonomic work for this paper was done by S. I. GOLOVATCH (cf. GOLOVATCH, 1992a, b), the evaluation of field data by J. ADIS and S. HAMANN. Diplopoda sampled were classified as juveniles (7, 9, 12, 15, 17 and 18 pairs of legs), subadults (19 pairs of legs) and adults (20 pairs of legs) according to SCHUBART (1934). Sex was determined in the adults.

RESULTS AND DISCUSSION

About 2600 specimens of *Cutervodesmus adisi* Golovatch, 1992 were collected in the seasonal blackwater inundation forest under study. Of these, 98% could be grouped into developmental stages. The majority were juveniles (97.1% of the total catch; n = 2420), 1.7% were subadults (n = 43) and 1.2% adults (n = 29).

C. adisi represented 60.4% (329 ind. m^{-2} $month^{-1}$) of all Diplopoda (545 ind. m^{-2} $month^{-1}$) extracted from soil samples during the non-inundation period 1981/82. A total of 7.2 ± 4.0 millipedes per m^2 (1.4 ind. m^{-2} $month^{-1}$) were collected on the soil surface during the non-inundation period in 1976/77. Animals occurred solely from January to April (rainy season) in ground photo-eclectors and were not detected during the preceding dry season. Out of these, *C. adisi* represented 4.5 ±0.7 ind. m^{-2} (= 62.5 %; 0.9 ind. m^{-2} $month^{-1}$). The majority of the total diplopods obtained in 1976/77 was sampled on tree trunks (cf. Table 5 *in* ADIS, 1981): out of

Source : MNHN, Paris

the 13516 specimens caught, 17.5% (n = 2369) were represented by *C. adisi*. It was the eudominant species of all Polydesmida collected (n = 566l) and represented 41.9% of their total catch. The percentage of trunk ascending individuals of *C. adisi* was higher (28.2% of the total Diplopoda and 66.7% of all Polydesmida caught), when compared to trunk descending animals (15.1% of the total Diplopoda and 36.1% of all Polydesmida sampled).

C. adisi reaches 6.0 mm in length (cf. GOLOVATCH, 1992a). The species is considered hemiedaphic, as 94% of all specimens extracted from soil samples in 1981/82 were found in the top 7 cm (Fig. 1), independent of seasons. This becomes evident, when significant correlations between the abundance of *C. adisi* and different soil conditions in the study area are carefully analysed.

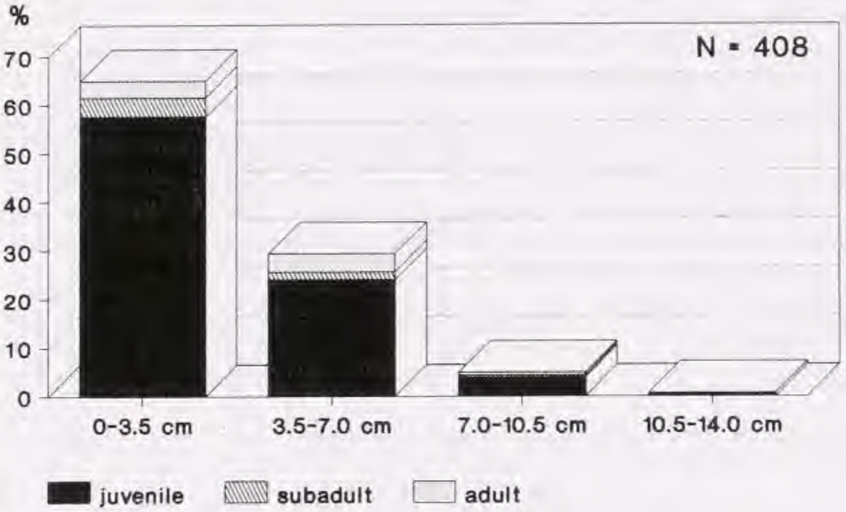


FIG. 1. — Distribution of developmental stages of *Cutervodesmus adisi* in the soil at Rio Tarumã Mirím. Monthly samples taken every 3.5 cm to a depth of 14 cm between September, 1981 and February, 1982 (non-inundation period); total catch = 100%.

During the dry season the decreasing abundance with greater soil depth was positively correlated with the increasing soil moisture content (e.g. Nov. 19, 1981: $p < 0.01$, $r = +0.9924$ for the total catch and $p < 0.05$, $r = +0.9798$ for juveniles; $n = 4$, respectively). However, during the rainy season, particularly after heavy rainfalls, the decreasing abundance was negatively correlated with the now decreasing soil moisture content in greater soil depth (e.g. Dec. 17, 1981: $p < 0.001$, $r = -0.9995$ for juveniles; $n = 4$). Similar changes were found with regard to soil temperatures: an increase with greater soil depth after heavy rainfalls was negatively correlated with the decreasing abundance of *C. adisi* ($p < 0.05$), whereas a temperature decrease with greater soil depth during dryer periods was positively correlated with the decreasing abundance of the species ($p < 0.05$).

Grain size and mineral composition of the soil seem to be especially important for the vertical distribution of terricolous arthropods in seasonal inundation forests (cf. ADIS *et al.*, this volume). First analyses of soil data (ADIS & IRION, unpubl.) indicated, that the decreasing abundance of *C. adisi* with greater soil depth during the dry and rainy seasons corresponded with an increasing amount of grains > 1000 µm in lower soil layers (from 0.7% in 0-3.5 cm to 2.7% in 10.5-14 cm depth; $p < 0.05$) and with a decreasing amount of silt from 14.6% in the top 3.5 cm to 10.8% in 14 cm soil depth ($p < 0.05$).

During the rainy season the decreasing abundance of *C. adisi* was negatively correlated with the increasing pH in lower soil layers as well ($p < 0.05$).

About 85% of the *C. adisi* population extracted from soil samples in 1981/82 was represented by juveniles, 7% by subadults and 8% by adults (Fig. 2). The sex ratio of males and females was 1:1.5 (n = 27). Adults and early larval stages (7, 9 & 12 segments) occurred solely in the soil (Fig. 3) where reproduction must have taken place.

Source : MNHN, Paris

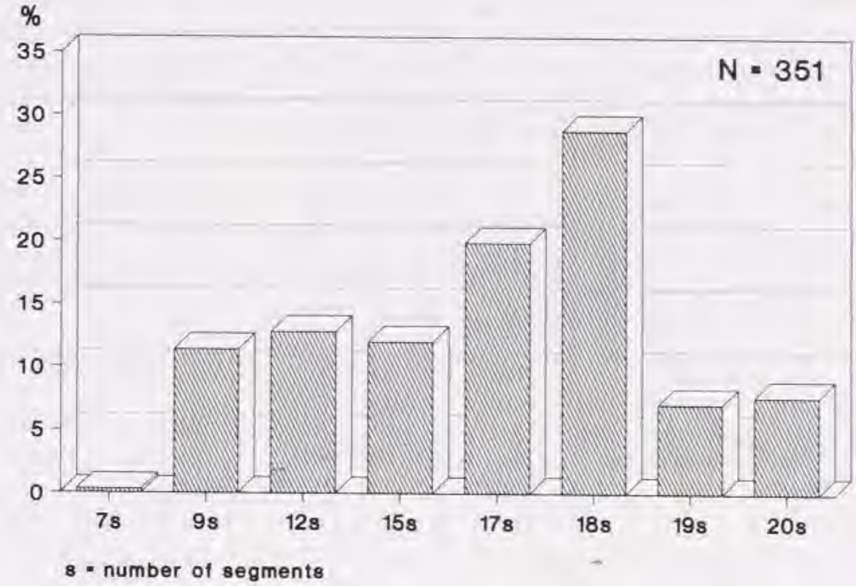


FIG. 2. — Percentage of developmental stages of *C. adisi* caught in the soil (0-14 cm depth). Monthly samples taken between September, 1981 and February, 1982 (non-inundation period) at Rio Tarumã Mirím.

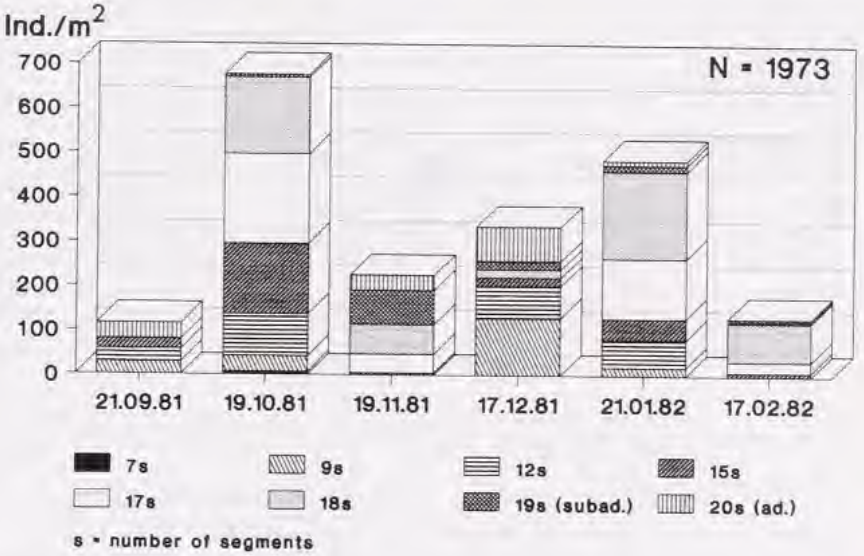


FIG. 3. —Temporal occurrence and abundance of *C. adisi* (ind./m2) in the soil (0-14 cm depth). Monthly samples taken between September, 1981 and February, 1982 (non -inundation period) at Rio Tarumã Mirím.

Advanced juvenile stages (the majority with 18 segments, some with 17 segments; cf. Table 1) were found to pass the inundation period in the trunk region (Figs 4, 5) and to recolonize the forest floor after the floodwater had receded. In 1981, some animals had already moulted to adults and reproduced within the first five weeks after the forest floor had dried, as juvenile stages of the offspring occurred from mid-September onwards (Fig. 3). Abundance of *C. adisi* in the soil was highest during the dry season (October 19, 1981: 678 ind. m-2). The first larval stage of the progeny (7 segments, 3 pairs of legs) was obtained at this time only and is believed to be of short duration (cf. HOPKIN & READ, 1992). In 1981/82, 49% of all *C. adisi* specimens extracted from soil samples comprised advanced juvenile stages with 18 segments and to a lesser extent with 17 segments (Fig. 2). They represented "migratory stages" which came to the soil surface at the beginning rainy season and started ascending tree trunks (Fig. 4).

Source : MNHN, Paris

In 1976, they were caught in ground photo-eclectors from January onwards, and activity density became greater with an increasing water saturation of the soil during subsequent weeks ($p < 0.05$, $r = +0.521$; $n = 16$; Fig. 4). Shortly before forest inundation, abundance of *C. adisi* in the soil was lowest (131 ind. m^{-2}; Fig. 3). The juveniles of non-migrating stages remaining in the soil were forced into the trunk area by the inundation of the forest (Table 1). Similar behaviour was found in two species of pseudoscorpions, and where tritonymphs represented the migratory stage (ADIS & MAHNERT, 1985; ADIS *et al.*, 1988).

TABLE 1.— Number (ind.) and dominance (%) of developmental stages of *Cutervodesmus adisi* caught during trunk ascents (BE↑) and trunk descents (BE↓) on three different tree species of Leguminosae in different years (capture periods: BE↑ from December to May in 1975/76, 1976/77, 1982/83 & 1983/84; BE↓ from July to October, 1976). No specimens were captured on *Mora paraensis* DUCKE (Caesalpiniaceae) between July and October, 1976. N.I. = No Investigation.

Trunk ascent (BE ↑)	Stage	1975/1976	1976/1977	1982/1983	1983/1984	Total	
		N	N	N	N	N	%
Aldina latifolia	15	–	–	1	–	1	1.1
Benth var. *latifolia* I	17	–	–	5	3	8	8.4
(Fabaceae)	18	3	3	14	52	72	75.8
	19	–	–	13	1	14	14.7
	Total	3	3	33	56	95	100.0
Aldina latifolia	17	–	14	N.I.	N.I.	14	2.7
Benth var. *latifolia* II	18	29	476			505	97.3
(Fabaceae)	Total	29	490			519	100.0
Peltogyne venosa	17	1	1	N.I.	N.I.	2	1.2
Benth ss. *densiflora* (Benth) M. Silva	18	25	138			163	98.8
(Caesalpiniaceae)	Total	26	139			165	100.0

Trunk descent (BE↓)	Stage	1976		SUM	Trunk ascent		Trunk descent		Total	
		N	%	Stage	N	%	N	%	N	%
Aldina latifolia Benth var. *latifolia* III (Fabaceae)	17	252	23.1							
	18	837	76.9	15	1	0.1	–	–	1	0.1
	Total	1089	100.0	17	24	3.1	273	20.5	297	14.1
Aldina latifolia Benth var. *latifolia* IV (Fabaceae)	17	21	8.7	18	740	95.0	1057	79.5	1797	85.2
	18	220	91.3	19	14	1.8	–	–	14	0.7
	Total	241	100.0	Total	779	100.0	1330	100.0	2109	100.0

In *C. adisi* the number of migratory juveniles caught in arboreal photo-eclectors was higher during periods of less insolation (February-May 1977: $p < 0.01$, $r = -0.9914$, $n = 4$; cf. Fig. 4). This was also reported for trunk ascending adults of *Hanseniella arborea*, a migrating symphylan in seasonal mixed- and blackwater inundation forests (ADIS *et al.*, this volume). During rainy seasons which showed an approximately equal amount of precipitation between months and a steady increase of flood waters in the study area, trunk ascents of *C. adisi* occurred over a long period of time, e.g. from December to April in 1983/84. They were relatively short in duration during rainy seasons which were marked by a greater amount of rainfall in certain months and by fast rising flood waters, e.g. in February/March 1976 and in April/May 1983. These two years were characterized by macroclimatic El Niño-Southern Oscillation (ENSO) events (strong in 1982/83 and weaker in 1976/77), which were statistically shown to cause a decrease in total precipitation during the rainy season in Central Amazonia and a lower average water-level of the Rio Negro seven months after the event had begun (ADIS & LATIF, 1995; cf. ROPELEWSKI & HALPERT, 1987; PHILANDER, 1983; RICHEY *et al.*, 1989).

Source : MNHN, Paris

From December 1982 until May 1983 (Fig. 5) the trunk ascent in *C. adisi* was significantly correlated with the rising water gauge of the Rio Negro at Manaus ($p < 0.05$, $r = +0.8380$; $n = 6$).

C. adisi is believed to be nocturnal as it was found to pass the flood period aggregated under loose bark of trunks during the day. The number of specimens caught on individual trees of the same and of different tree species varied considerably (cf. Table 1) and tree trunks with smooth and/or thin bark may be avoided (e.g. *Mora paraensis*). In 1977, trunk descents were observed to occur within 1-2 weeks and at the time when the forest floor was about to emerge from the receding floodwater (cf. Fig. 4).

C. adisi was neither detected in tree crowns (by means of canopy fogging) nor in epiphytes (5-25 m above ground), nor was it found in flooded soils which were taken from under the water during forest inundation. Adults and early juvenile stages occurred solely on the forest floor. Based on the characteristics outlined, *C. adisi* represents a terricolous, migrating and univoltine species, which is considered endemic of seasonal blackwater inundation forests in the Rio Negro valley. Vertical migration of advanced juvenile stages represents an ethological adaptation to escape annual long-term flooding, which was not found in Polydesmida and other terrestrial invertebrates of neighbouring non-flooded upland forests (cf. ADIS, 1992a; GOLOVATCH, 1992a, b).

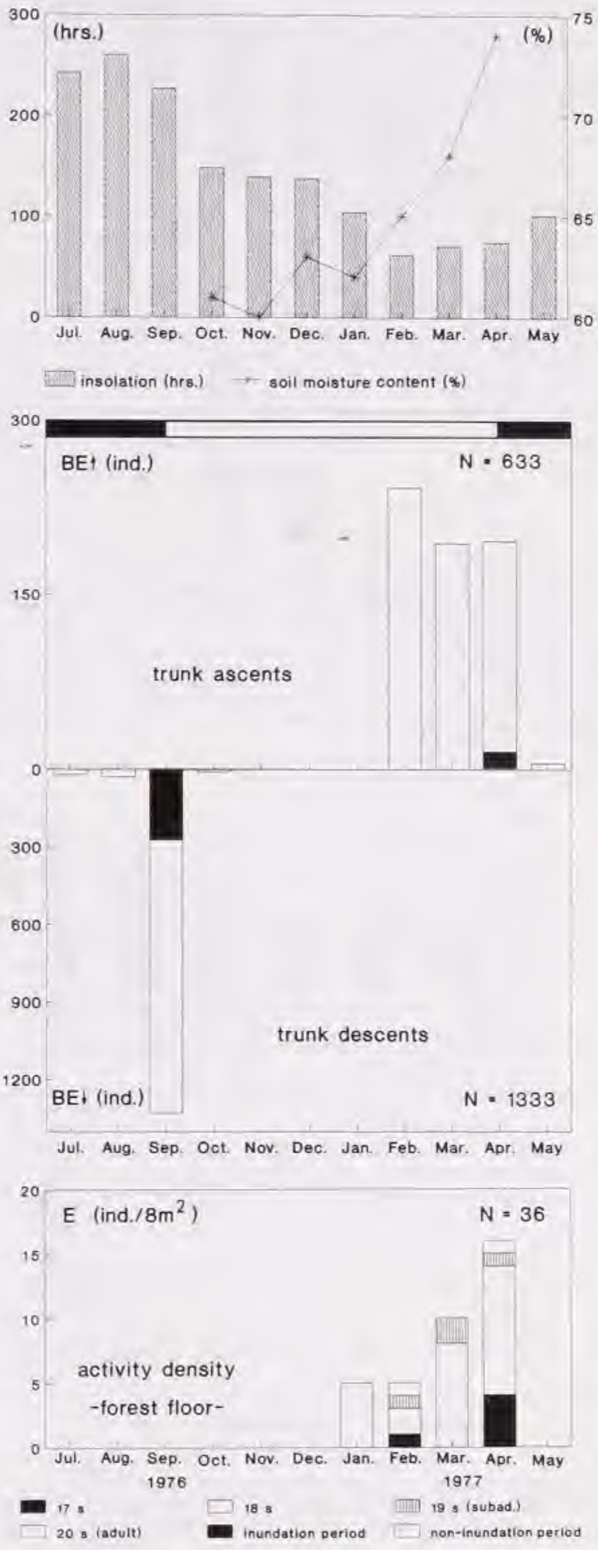


FIG. 4. — Activity density of *Cutervodesmus adisi* on the forest floor (8 ground photo-eclectors (E); ind./8m²), trunk descents (BE↓)and trunk ascents (BE↑); three arboreal photo-eclectors, respectively between July, 1976 and May, 1977 at Rio Tarumã Mirím. Soil moisture content is expressed as the percentage portion of the soil humidity (vol. %) at the maximal water capacity of the soil (= 34 vol. %; cf. ADIS, 1981).

Source : MNHN, Paris

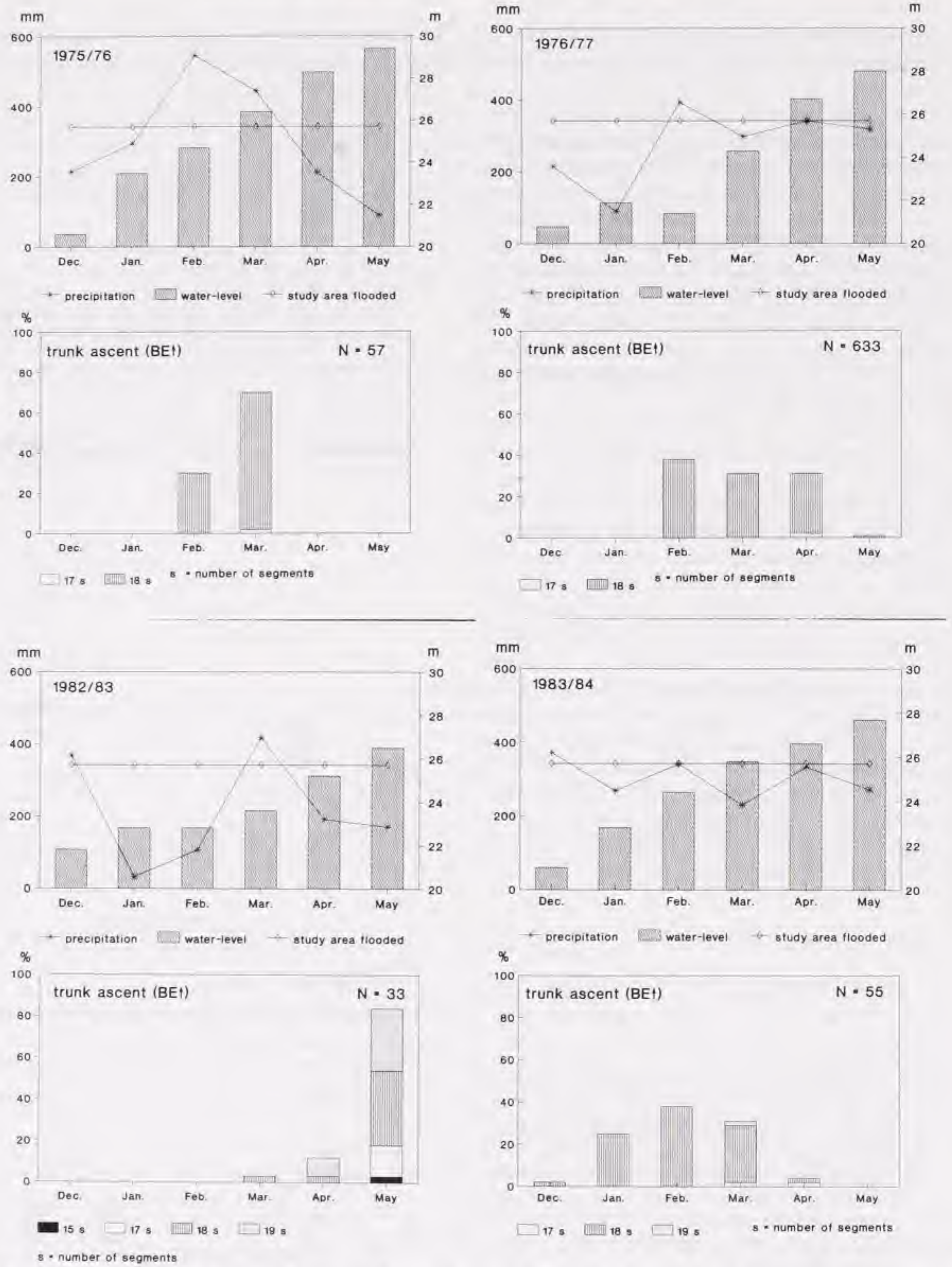


FIG. 5. — Percentage of developmental stages of *Cutervodesmus adisi* ascending trunks caught per month in arboreal photo-eclectors during four rainy seasons in relation to water-level of the Rio Negro and precipitation in the Manaus area; total catch per season = 100 %. (See left page).

Source : MNHN, Paris

The flood pulse is regarded as the original determinant of the upward and downward migrations of terrestrial invertebrates on tree trunks in the seasonal inundation forests of Central Amazonia (ADIS, 1992a). However, it is still the primary control mechanism or ecofactor only among certain species. Most of the invertebrates, like *C. adisi*, have apparently become sensitive to secondary, mainly abiotic ecofactors, which are no longer directly related to the cycle of flooding. The migration of animals from the ground to tree trunks (and their flight to upland forests) is triggered mainly by the rainy season (December - May), which begins three to four months before the flooding, and by the changes in the edaphic and climatic factor it causes.

Following GOLOVATCH's (1987) proposed division of the Diplopoda into morphotypes and ecomorphotypes (= life-forms), *C. adisi* represents a good climber: its body is fairly small (up to 6 mm in length with females being larger (5.0-6.0 mm) than males (4.5-5.3 mm)), the paraterga are relatively small, the legs relatively strong and not too slender, with the somewhat pretarsal podomeres and more slender and long tarsi each crowned with a well-developed claw. Such a morphological pattern also fits a soil dweller (= edaphobiont), which is also the case. The high number of migratory stages (which represented almost half the population in the soil), the probable predominance of females on the forest floor and the synchronization of reproduction in the soil with the non-inundation period compensates for the decline in population density during flooding and assures the persistence of this species in a harsh environment.

ACKNOWLEDGEMENTS

We are indebted to all our colleagues at the National Institute of Amazonian Research (INPA) in Manaus (Brazil) and at the Max-Planck-Institute for Limnology in Plön (Germany) who, in the field or laboratory, contributed to this study, especially Edilson DE ARAUJO SILVA, M. Sc. Elizabeth FRANKLIN, M. Sc. José Wellington DE MORAIS and Irmgard ADIS. This study was supported by a grant from the Max-Planck-Society for the second author. We wish to acknowledge the valuable support received by PD Dr. W. J. JUNK, head of the Tropical Ecology Working Group at the Max-Planck-Institute for Limnology in Plön, Germany. Dr. Helen READ (Bucks, United Kingdom) and Dr. Ulf SCHELLER (Järpås, Sweden) kindly corrected the English manuscript.

REFERENCES

ADIS, J., 1979. — Problems of interpreting arthropod sampling with pitfall traps. *Zool. Anz.*, **202** : 177-184.

ADIS, J., 1981. — Comparative ecological studies of the terrestrial arthropod fauna in Central Amazonian inundation forests. *Amazoniana*, **7** : 87-173.

ADIS, J., 1984. — 'Seasonal Igapó'-forests of Central Amazonian blackwater rivers and their terrestrial arthropod fauna. *In*: H. SIOLI, *The Amazon. Limnology and landscape ecology of a mighty tropical river and its basin.* Monographiae Biologicae, Dordrecht, W. Junk Publ. : 245-268.

ADIS, J., 1986. — An "aquatic" millipede from a Central Amazonian inundation forest. *Oecologia*, **68** : 347-349.

ADIS, J., 1987. - Extraction of arthropods from Neotropical soils with a modified KEMPSON apparatus. *J. trop. Ecol.* , **3** : 131-138.

ADIS, J., 1992a. — Überlebensstrategien terrestrischer Invertebraten in Überschwemmungswäldern Zentralamazoniens. *Verh. naturwiss. Ver. Hamburg*, **33** : 21-114.

ADIS, J., 1992b. — How to survive six months in a flooded soil : Strategies in Chilopoda and Symphyla from Central Amazonian floodplains. *In*: : J. ADIS & S. TANAKA, *Symposium on life-history traits in tropical invertebrates.* [INTECOL, Yokohama, Japan 1990. *Studies on Neotropical Fauna and Environment*, **27**]. Lisse, Swets & Zeitlinger : 117-129.

ADIS, J., 1992c. — On the survival strategy of *Mestosoma hylaeicum* Jeekel (Paradoxosomatidae, Polydesmida, Diplopoda), a millipede from Central Amazonian floodplains. *Ber. nat.-med. Ver. Innsbruck*, **Suppl. 10** : 183-187.

ADIS, J. & LATIF, M., 1995. — Amazonian arthropods respond to El Niño. *Biotropica* : (in press).

ADIS, J. & MAHNERT, V., 1985. — On the natural history and ecology of Pseudoscorpiones (Arachnida) from an Amazonian blackwater inundation forest. *Amazoniana*, **9** : 297-314.

ADIS, J. & SCHUBART, H. O. R., 1984. — Ecological research on arthropods in Central Amazonian forest ecosystems with recommendations for study procedures. *In*: J. H. COOLEY & F. B. GOLLEY, *Trends in ecological research for the 1980s.* [NATO Conference Series, Series I : Ecology] New York, London, Plenum Press : 111-144.

ADIS, J., LUBIN, Y. D. & MONTGOMERY, G.G., 1984. — Arthropods from the canopy of inundated and terra firme forests near Manaus, Brazil, with critical considerations on the pyrethrum-fogging technique. *Studies on Neotropical Fauna and Environment*, **19** : 223-236.

Source : MNHN, Paris

ADIS, J., MAHNERT, V., MORAIS, J. W. DE & RODRIGUES, J. M. G., 1988. — Adaptation of an Amazonian pseudoscorpion (Arachnida) from dryland forests to inundation forests. *Ecology*, **69** : 287-291.

BECK, L., 1976. — Zum Massenwechsel der Makro-Arthropodenfauna des Bodens in Überschwemmungswäldern des zentralen Amazonasgebietes. *Amazoniana*, **6** : 1-20.

CAVALLI-SFORZA, L., 1972. — *Grundzüge biologisch-medizinischer Statistik*. Stuttgart, G. Fischer, 212 pp.

ERWIN, T. L., 1983. — Beetles and other insects of tropical forest canopies at Manaus, Brazil, sampled by insecticidal fogging. X. *In*: S. L. SUTTON, T. C. WHITMORE & A. C. CHADWICK, *Tropical Rain Forest: Ecology and Management*. Oxford, Blackwell Scientific Publications : 59-75.

FUNKE, W., 1971. — Food and energy turnover of leaf-eating insects and their influence on primary production. *Ecological Studies*, **2** : 81-93.

GOLOVATCH, S. I., 1987. — On life-forms in millipedes (Diplopoda). *In*: B. R. STRIGANOVA, *Soil fauna and soil fertility*. Moscow, Nauka : 210-213.

GOLOVATCH, S. I., 1992a. — Review of the Neotropical fauna of the millipede family Fuhrmannodesmidae, with the description of four new species from near Manaus, Central Amazonia, Brazil (Diplopoda, Polydesmida). *Amazoniana*, **12** : 207-226.

GOLOVATCH, S. I., 1992b. — Review of the Neotropical millipede genus *Onciurosoma* SILVESTRI, 1932, with the description of three new species from near Manaus, Central Amazonia, Brazil (Diplopoda, Polydesmida, Paradoxosomatidae). *Amazoniana*, **12** : 227-237.

HOFFMAN, R. L., 1984. — A new species of *Epinannolene* from the Amazon Basin, Brazil (Spirostreptida: Pseudonannolenidae). *Myriapodologica* , **1** : 91-94.

HOFFMAN, R. L., 1985. — A new milliped of the genus *Gonographis* from an inundation forest near Manaus, Brazil (Pyrgodesmidae). *Amazoniana*, **9** : 243-246.

HOPKIN, S. P. & READ, H. J., 1992. — *The biology of millipedes*. Oxford, Oxford Univ. Press, 233 pp.

JUNK, W. J., BAYLEY, P. B. & SPARKS, R. E., 1989. — The flood pulse concept in river-floodplain systems. *Can. Spec. Publ. Fish. Aquatic. Sci.*, **106** : 110-127.

MAURIÈS, J.-P., 1984. — Les premiers Stemmiulides signalés au Brésil : trois espèces nouvelles de la région de Manaus, dont une de la forêt inondable (*Prostemmiulus adisi* n. sp.)(Myriapoda : Diplopoda : Stemmiulida). *Amazoniana*, **8** : 375-387.

MESSNER, B. & ADIS, J., 1988. — Die Plastronstrukturen der bisher einzigen submers lebenden Diplopodenart *Gonographis adisi* Hoffman 1985 (Pyrgodesmidae, Diplopoda). *Zool. Jb. Anat.*, **117** : 277-290.

MEYER, U., 1991. — Feinwurzelsysteme und Mykorrhizatypen als Anpassungsmechanismen in zentralamazonischen Überschwemmungswäldern - Igapó und Várzea. Univ. Hohenheim, FR Germany: Ph.D.-thesis, 223 pp.

PHILANDER, S. G. H., 1983. — El Niño Southern Oscillation phenomena. *Nature*, **302** : 295-301.

PRANCE, G. T., 1979. — Notes on the vegetation of Amazonia III. The terminology of Amazonian forest types subject to inundation. *Brittonia*, **31** : 26-38.

RIBEIRO, M. DE N. G. & ADIS, J., 1984. — Local rainfall variability - a potential bias for bioecological studies in the Central Amazon. *Acta Amazonica*, **14** : 159-174.

RICHEY, J. E., NOBRE, C. & DESER, C., 1989. — Amazon River discharge and climate variability: 1903-1985. *Science*, **246** : 101-103.

ROPELEWSKI, C. F. & HALPERT, M. S., 1987. — Global and regional scale precipitation patterns associated with the El Niño/Southern Oscillation. *Mon. Wea. Rev.*, **115** : 1606-1626.

SCHUBART, O., 1934. — Tausendfüssler oder Myriapoda I: Diplopoda. *In*: F. DAHL, *Tierw. Deutschl.* **28**, Jena, G. Fischer, 1-318.

WORBES, M., 1986. — Lebensbedingungen und Holzwachstum in zentralamazonischen Überschwemmungswäldern. *Scripta Geobotanica*, **17** : 1-112.

Source : MNHN, Paris

Cycles d'activité comparés de populations de diplopodes édaphiques dans un écosystème forestier tempéré

Jean-Jacques GEOFFROY * & *Marie-Louise* CÉLÉRIER **

* CNRS, Muséum National d'Histoire Naturelle, IEGB, Laboratoire d'Ecologie Générale
4, avenue du Petit Château F-91800 Brunoy, France
** Université Pierre & Marie Curie, Boîte 6, UFR Sciences de la Vie, Bât. A
4, place Jussieu F-75252 Paris Cedex 05, France

RÉSUMÉ

Le cycle d'activité de cinq espèces du peuplement de diplopodes édaphiques d'un écosystème forestier du Bassin Parisien (Station Biologique de Foljuif, Seine-et-Marne, France) a été suivi à l'aide de pièges d'interception durant plusieurs années. Cette étude permet de déterminer l'importance relative des fractions adultes et juvéniles des populations dans les couches supérieures de litière (couche L et couche F) au cours des diverses périodes caractérisant le cycle annuel. Outre la mise en évidence des phases successives de colonisation des nouvelles couches de litière par des populations fonctionnellement complémentaires, cette approche, qui prend en compte les variations interannuelles, conduit à sélectionner les catégories d'individus qui interviennent de manière fondamentale dans l'organisation d'un groupe fonctionnel de "macrodiplopodes saprophages".

ABSTRACT

Compared Activity Cycles of Millipede Populations in a Temperate Woodland Ecosystem.

The activity cycle of five species mainly representative of the edaphic millipede community have been investigated in a temperate woodland ecosystem belonging to the Fontainebleau Forest (Foljuif Biological Station, Seine-et-Marne, France). The research has been conducted using Barber Pitfall Traps (PT) during several successive years. This study allows to estimate the relative importance of the adult and juvenile fractions of specific populations acting in the upper litter layers of the Oak (*Quercus petraea*) and Hornbeam (*Carpinus betulus*) forest (L layer and F layer). The situation has been examined during the characteristic successive periods of the annual cycle. This investigation contributes to distinguish obvious steps in the colonization of recently fallen leaves by millipede populations and individuals, showing complementary ecological functions and migrating activity in the litter layers. Considering interannual variations, it is possible to select individuals that play an important role in the composition and organization of a "functionnal saprophagous macro-diplopod group". The investigated species are two short-cycle ones : *Melogona gallica* (Latzel) and *Polydesmus angustus* Latzel, and three long-lived ones: *Glomeris marginata* (Villers), *Cylindroiulus punctatus* (Leach) and *Allajulus nitidus* (Verhoeff).

GEOFFROY, J.-J. & CÉLÉRIER, M.-L., 1996. — Cycles d'activité comparés de populations de diplopodes édaphiques dans un écosystème forestier tempéré. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 533-554. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

INTRODUCTION

De nombreux types de pièges, de conception et de forme variées, ont été employés pour la capture qualitative et semi-quantitative des invertébrés (PARK, 1935 ; JOOSE & KAPTEIJN, 1968 ; LE BERRE, 1969 ; SOUTHWOOD, 1978 ; DRACH *et al.*, 1981 ; PANTIS *et al.*, 1988). Dans le cas des Macroarthropodes terrestres de forêt tempérée, on utilise le plus souvent des pièges d'interception constitués de pots enfoncés dans le sol, dérivés de la technique mise au point par BARBER (1931) pour l'étude d'insectes cavernicoles (DRIFT, 1951 ; GIST & CROSSLEY, 1973 ; LUFF, 1975). On fait largement usage des pièges d'interception dans l'étude d'animaux particulièrement mobiles tels que les coléoptères (BRIGGS, 1961 ; MURDOCH, 1966 ; MADER & MÜHLENBERG, 1981 ; FRANKE & FRIEBE, 1983 ; FRIEBE, 1983 ; LECORDIER & BENEST, 1986 ; RUSDEA, 1992). De nombreux auteurs ont été amenés à interpréter les cycles d'activité de diplopodes à l'aide de cette technique bien adaptée à des animaux se déplaçant entre les interstices que forment les constituants organiques des litières forestières et capables de migrations actives entre les différents compartiments édaphiques (Tableau 1). De façon générale, la technique des pots-pièges enfoncés renseigne sur les périodes d'activité des populations envisagées à l'échelle de la journée (PARK *et al.*, 1931 ; PARK, 1935 ; WILLIAMS, 1958, 1959 ; BANERJEE, 1967a ; DONDALE *et al.*; 1972) ou au cours des phases saisonnières lors d'études portant au minimum sur un cycle annuel (GILBERT, 1956 ; GREENSLADE, 1964 ; MURDOCH, 1966 ; BANERJEE, 1967a, b).

Les études par piégeage ne comportent un aspect véritablement quantitatif que dans quelques expériences particulières (BANERJEE, 1970 ; GIST & CROSSLEY, 1973). Elles cherchent à montrer l'existence de relations entre l'activité locomotrice des individus et la densité des populations durant la période de capture (MITCHELL, 1963 ; GREENSLADE, 1964 ; BLOWER, 1970 ; ADIS, 1979 ; DAVID & POUSSARDIN, 1983). Divers auteurs s'accordent à placer ce type de relations dans le cadre du concept d'activité-densité (KACZMAREK, 1978) qui traduirait la capacité moyenne des individus à effectuer des déplacements (BANERJEE, 1970 ; DAVID, 1983 ; COURET, 1985 ; FRANKE *et al.*, 1988). Si des données semi-quantitatives liées à l'abondance des populations sont ainsi acquises, elles ne portent cependant que sur une fraction de celles-ci, celle qui est capable de se déplacer horizontalement et entre les couches constituant la litière. Les larves de premiers stades, sédentaires et rarement représentées dans les couches supérieures de litière, de même que les individus en cours de mue, échappent en grande partie à ce type de mesure. En revanche, les formes subadultes et adultes y sont bien adaptées.

Pour cette raison, la technique présente un intérêt supplémentaire, en contribuant à séparer deux groupes d'individus jouant des rôles différents à l'intérieur d'un ensemble taxinomiquement homogène. De plus, associé à d'autres méthodes de capture, le piégeage d'interception permet de localiser dans le temps certains phénomènes liés à la biologie des adultes reproducteurs (BLOWER, 1978 ; DAVID & POUSSARDIN, 1983 ; DAVID, 1984).

Sans perdre de vue les limites imposées par l'emploi des pièges d'interception dans les programmes de recherche en écologie des peuplements (TOPPING & SUNDERLAND, 1992), le propos de ce travail est de décrire les cycles d'activité des principales espèces de diplopodes d'un sol forestier, cherchant à déterminer, pour chaque saison, quelle fraction du peuplement fréquente majoritairement les couches les plus superficielles de la litière (L+F). Le piégeage permet en outre de situer dans le temps les phases de mobilité des adultes mâles et femelles liées à des activités de reproduction, de consommation ou de migration (DRIFT, 1951 ; BARLOW, 1958 ; BLOWER, 1970 ; COTTON & MILLER, 1974 ; DAVID & POUSSARDIN, 1983). Enfin, à condition d'étendre l'opération sur plusieurs années, cette méthode d'étude contribue à mettre en évidence des fluctuations significatives dans l'importance relative des populations et, par là-même, dans la structure du peuplement lié aux couches holorganiques du sol.

Cette étude se situe en amont d'un programme de recherche à long terme mené sur les communautés édaphiques d'un écosystème forestier (BLANDIN *et al.*, 1980, 1985 ; GEOFFROY

Source : MNHN, Paris

et al. 1981, 1987). Elle s'intègre aux données quantitatives obtenues tant sur les diplopodes (GEOFFROY, 1981a, 1985) que sur des groupes écologiquement complémentaires tels que les isopodes oniscoïdes (MOLFETAS, 1982) ou les larves de diptères (MOLLON, 1982, 1983) et aux recherches menées sur la dynamique de la transformation des matériaux organiques lors des phases de colonisation par la faune édaphique (GARAY *et al.* 1986a, b). En outre, cette présentation des cycles d'activité des diplopodes de la forêt de Foljuif s'insère dans une étude des variations pluriannuelles de l'abondance des populations (GEOFFROY, *in prep.*).

TABLEAU 1. — Sélection des travaux relatifs à l'activité des populations de diplopodes édaphiques, menés à l'aide de pièges d'interception de type Barber (PT).
TABLE 1. — Some selected studies dealing with soil millipede population activity, investigated by Barber Pitfall Traps (PT).

REFERENCES	ECOSYSTEM	LOCALITY	COUNTRY
ADIS 1979	Beech forest	Solling, Göttingen	FRG
ALBERT 1978	Mixed forests	Wuppertal	FRG
BAKER 1979, 1985, 1988	Sclerophyllous Forests & Grasslands	Aust. South-West	Australia
BANERJEE 1967a,b	Oak forest	Roy. Holloway College	UK
BARLOW 1957, 1958	Dunes and forests	Meijendel Dune, Leiden	Netherlands
BLOWER 1970	Sycamore / ash wood	Ernocroft, Cheshire	UK
COTTON & MILLER 1974	Sand dunes	Marram Dune,Tentsmuir	UK
COURET 1985	*Quercus petraea* & *Pinus sylvestris*	Orléans Forest	France
DAVID & POUSSARDIN 1983	*Quercus petraea* & *Pinus sylvestris*	Orléans Forest	France
DETHIER & PEDROLI-CHRISTEN 1983	Alpine grassland	Mt La Schera, Grisons	Switzerland
DRIFT VAN DER 1951	Beech forest	NP de Hooge Veluwe	Netherlands
FAIRHURST 1979	Sand dune	Gibraltar Pt, Lincolnsh.	UK
GILLON & GILLON 1976	Grassland & savannah	Darou (Kaolack)	Senegal
HAACKER 1968	Different ecosystems	Rhein-Main-Gebiert	FRG
JANATI-IDRISSI 1988	*Brachypodium* grassplot	St-Gely-du-Fesc	France
KORSOS 1991	Dolomitic grassland	Buda Mts	Hungary
KURNIK 1985	Subalpine grassland to nival zone	Großglockner	Austria
KURNIK 1988	Xerothermic & agricultural sites	Albeins : South Tyrol	Austria
KURNIK & THALER 1985	Mixed oak forest	Stams, North Tyrol	Austria
LOKSA 1988	Mixed grassland & forest sites	Pilis Mountains	Hungary
MEYER 1979	Mountain to alpine ecosystems	Ötzal	Austria
MEYER 1980, 1985	Mountain to alpine ecosystems	Obergurgl	Austria
PEDROLI-CHRISTEN 1981	Mountain & subalpine forests	Swiss Jura	Switzerland
PEDROLI-CHRISTEN & SCHOLL 1990	Mountain & subalpine forests	Swiss Jura	Switzerland
SPELDA 1993	Coniferous forests	Oberreichenbach	FRG
SZEKELYHIDY & LOKSA 1979	Oak forets (*Q. petraeae - cerris*)	"Sikfökút Projekt"	Hungary
VAJDA & HORNUNG 1991	Sandy grassland	Kiskunság natl. Park	Hungary

MILIEU D'ÉTUDE ET MÉTHODES

La forêt mixte de Foljuif (Massif de Fontainebleau, Seine-et-Marne, France) se situe à 80 km au Sud-Est de Paris. Elle présente deux zones principales qui diffèrent par la composition spécifique de leurs peuplements végétaux. Les essences dominantes sont le charme, *Carpinus betulus* L., et le chêne sessile, *Quercus petraea* (Mattus.) Liebl. dans la première zone, le pin sylvestre, *Pinus sylvestris* L., et le chêne sessile, *Q. petraea* (Mattus.) Liebl. dans la seconde. Les différences notables dans la chute des matériaux au sol induisent plusieurs types d'humus : un moder dans la zone 1 et un dysmoder dans la zone 2 (BLANDIN *et al.*, 1980 ; GARAY, 1980). Dans la station à moder, trois couches de litière existent tout au long de l'année : couches L, F et H, au sein desquelles la décomposition des feuilles est achevée au bout de trois ans (GARAY *et al.*, 1986a). Le programme de piégeage a été conduit dans la station à moder de la zone 1 sous chêne (*Q. petraea*) et charme (*C. betulus*).

Chaque piège est constitué d'un pot de matière plastique de 130 mm de diamètre et de 90 mm de profondeur. A sa surface, un orifice de capture de 80 mm de diamètre est aménagé grâce à une plaque rectangulaire dont les bords s'insinuent au niveau de la couche H de la litière, évitant une rupture brutale entre l'environnement immédiat et l'orifice. On assure ainsi une position précise du bord supérieur du pot par rapport au substrat (GREENSLADE, 1964).

Source : MNHN, Paris

Les appareils ont été installés dans une placette protégée de la zone d'étude, en rangées parallèles de cinq pièges. La distance entre deux pots est de 1 m. Les batteries de cinq pièges, disposées en quinconce, sont équidistantes de 10 m.
La capture d'un spécimen résulte avant tout de l'interception naturelle de l'animal. Pour cela, le piège doit demeurer neutre, dépourvu à la fois de caractère attractif ou répulsif (GREENSLADE & GREENSLADE, 1971). Les individus capturés sont préservés dans un liquide de fixation neutre qui ne doit pas affecter la capture des espèces (LUFF, 1968). Nous avons employé un liquide peu volatile, qui ne gèle pas et assure une bonne conservation des animaux : l'éthylène-glycol (SZEKELYHIDY & LOKSA, 1979). Afin d'éviter une dilution par l'eau de pluie (FICHTER, 1941 ; STEINER *et al.*, 1963), chaque piège est équipé d'une plaque de protection. En dépit de certains risques de modification de capture (DUNGER & ENGELMANN, 1978), ce dispositif évite le rayonnement solaire et surtout la chute des débris organiques à l'intérieur des pièges (Fig. 1).

Les pièges ont fonctionné simultanément durant quatre ans selon les modalités présentées par le Tableau 2. Toutefois, l'arrêt temporaire du piégeage, de juillet à octobre 1975 explique l'absence de capture durant cette période sur les Figures 2 à 8.
Il est important de signaler ici que le cycle annuel 1976 a été marqué par des conditions climatiques très particulières, notamment par une sécheresse considérable qui s'est étendue d'avril à septembre et qui a eu des effets immédiats sur les abondances des populations édaphiques (BLANDIN *et al.*, 1980, 1985).
La durée moyenne séparant deux relevés est de 14 jours. Les animaux récupérés sont fixés dans l'alcool 70°. Le taux de capture par piégeage ("Trappability" : PANTIS *et al.*, 1988) résultant des 81 expériences réalisées est exprimé en nombre d'individus capturés pour 20 pièges-trappes et pour 14 jours (Ind/20 PT/14 D).

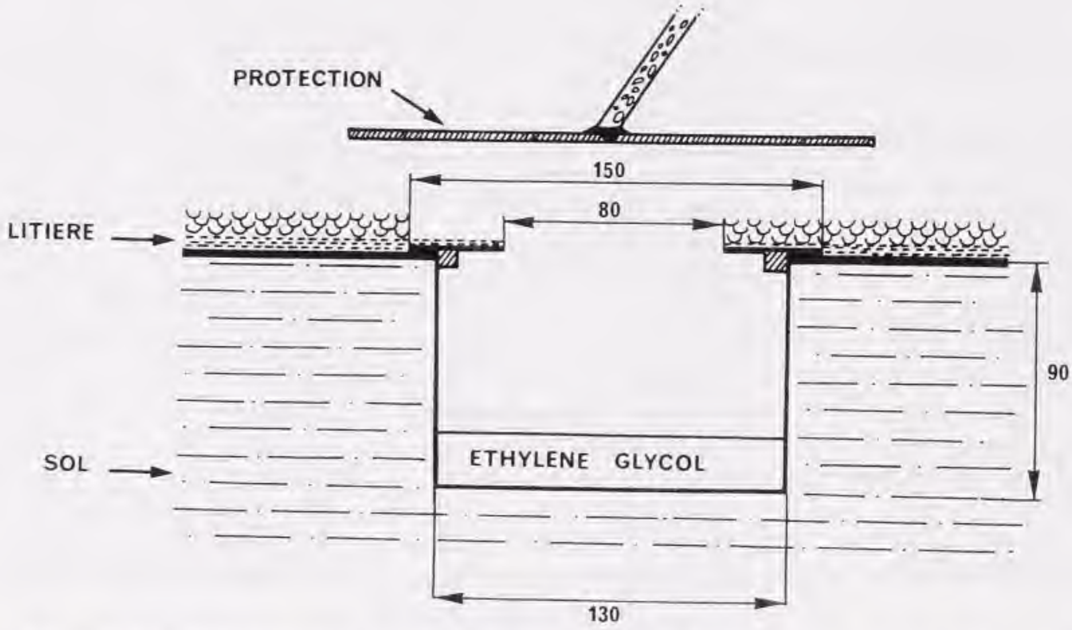


FIG. 1. — Un piège d'interception en place dans le sol en position ouverte. La limite de la capacité de capture correspond aux couches L et F de la litière.

FIG. 1. — A pitfall—trap in open—position in the soil of the temperate Foljuif Forest. The limit of catching efficiency corresponds to L and F litter layers.

RÉSULTATS

Diplopoda

Le peuplement global de diplopodes de la forêt de Foljuif est composé de 14 espèces parmi lesquelles 7 espèces sont fréquentes ou abondantes. Les cinq espèces dominantes sont :

Source : MNHN, Paris

- *Glomeris marginata* (Villers, 1789) [Glomerida, Glomeridea]
- *Melogona gallica* (Latzel, 1884) [Chordeumatida, Craspedosomatidea]
- *Polydesmus angustus* (Latzel, 1884) [Polydesmida, Polydesmidea]
- *Allajulus nitidus* (Verhoeff, 1891) [Julida, Julidea]
- *Cylindroiulus punctatus* (Leach, 1815) [Julida, Julidea]

auxquelles il faut ajouter :

- *Cylindroiulus caeruleocinctus* (Wood, 1864) [Julida, Julidea]
- *Ommatoiulus sabulosus* (Linné, 1758) [Julida, Julidea].

Seules ces espèces ont été collectées dans les pièges d'interception. Globalement, le cycle d'activité du peuplement présente deux pics. Le premier se situe au printemps, entre mai et juin, le second apparaît en automne, de fin-octobre à début décembre. Dans l'ensemble, les captures sont moins importantes durant l'hiver et le milieu de l'été. La même tendance saisonnière se répète durant les quatre cycles annuels successifs et traduit notamment la capacité de déplacement des adultes. En effet, les juvéniles sont toujours très faiblement représentés dans les pièges, même en période de recrutement des jeunes au début de l'été (Fig. 2).

Un cycle d'activité présentant deux maxima est souvent observé chez les diplopodes édaphiques (*e.g.* DUNGER & STEINMETZGER, 1981 ; PEITSALMI, 1981 ; MEYER, 1985) alors qu'une succession de trois pics est plus rarement mise en évidence chez certaines populations (VAJDA & HORNUNG, 1991).

Le rapport saisonnier entre les sexes est rarement disproportionné avec toutefois une légère surabondance des mâles adultes, traduisant la grande mobilité de ces derniers durant les périodes actives.

Le faible taux de capture observé en automne 1976 est manifestement dû à la sécheresse qui a marqué cette année-là. Remarquons toutefois que l'effet ne s'en fait pas sentir à long terme car le niveau d'activité observé en automne 1977 et en 1978 est sensiblement le même que celui qui caractérisait le cycle de 1975.

Les pics d'activité de printemps sont le plus souvent plus importants que ceux de l'automne, exception faite du printemps de 1977, dont le maxima plus faible traduit l'effet de la sécheresse de 1976 sur l'ensemble des espèces. On observe une réponse quasi-immédiate de l'activité des adultes de plusieurs espèces aux conditions climatiques très contrastées de cette année. Ainsi, le pic isolé de juillet 1976 (4 espèces) coïncide exactement avec une augmentation ponctuelle des précipitations à la même date. (cf. BLANDIN *et al.*, 1980, Fig. 1). De plus, on peut observer une richesse spécifique maximum au printemps, 7 espèces de mai à juin, régulièrement supérieure à celle de l'automne où l'on rencontre 4 espèces au plus (Fig. 3). Ce phénomène s'explique par l'activité manifestée au printemps par les espèces les moins fréquentes (*Ommatoiulus sabulosus* et *Cylindroiulus caeruleocinctus*) et par une absence relative de *Cylindroiulus punctatus* des couches supérieures de litière en automne. Ce Julide effectue alors une migration en direction des horizons plus profonds du sol mais se trouve encore en grande partie dans les bois morts en décomposition où il a passé la période estivale. C'est dans ce milieu très particulier que sont déposées la plus grande partie des pontes, qu'a lieu l'éclosion et que se déroule les premières étapes du développement post-embryonnaire (GEOFFROY, 1981b). Durant l'automne, l'activité la plus importante est partagée par *Glomeris marginata* et *Allajulus nitidus*, ce dernier occupant à ce moment toutes les couches de la litière. (GEOFFROY, 1981b, 1985). La période hivernale est caractérisée par un taux de capture moyen ou faible selon les années mais qui est associé à une richesse spécifique elle-même très faible. Cette période coïncide presque exclusivement avec l'activité de surface des adultes mâles et femelles du chordeumide *Melogona gallica* .

Source : MNHN, Paris

TABLEAU 2. — Programme de piégeage réalisé dans la forêt tempérée de Foljuif (zone 1) durant la phase initiale du programme de recherche, du 07.02.75 au 19.12.78 (séries 1 à 81). S = n° de série ; PT = nombre de pièges ; D = nombre de jours.

TABLE 2. — Pitfall trapping programme realized in the temperate Foljuif forest (zone 1) during the initial period of the research programme, from 07.02.75 to 19.12.78 (series 1 to 81). S = n° series ; PT = number of pitfall-traps ; D = number of days.

PÉRIODE	S	PT	D
07.02.75-21.02.75	01	20	14
21.02.75-21.03.75	02	20	28
21.03.75-04.04.75	03	20	14
04.04.75-18.04.75	04	20	14
19.04.75-17.05.75	05	20	28
17.05.75-29.05.75	06	20	12
29.05.75-12.06.75	07	20	14
12.06.75-04.07.75	08	20	22
15.10.75-29.10.75	09	20	14
29.10.75-13.11.75	10	20	15
13.11.75-28.11.75	11	20	15
28.11.75-12.12.75	12	20	14
12.12.75-29.12.75	13	20	17
29.12.75-10.01.75	14	20	12
10.01.75-23.01.76	15	20	13
23.01.76-06.02.76	16	20	14
06.02.76-20.02.76	17	20	14
20.02.76-05.03.76	18	20	16
05.03.76-19.03.76	19	20	14
19.03.76-02.04.76	20	20	14
02.04.76-15.04.76	21	20	13
15.04.76-30.04.76	22	20	15
30.04.76-15.05.76	23	20	15
15.05.76-28.05.76	24	20	13
28.05.76-11.06.76	25	20	14
11.06.76-25.06.76	26	20	14
25.06.76-08.07.76	27	20	14
08.07.76-22.07.76	28	20	14
22.07.76-19.08.76	29	20	28
19.08.76-17.09.76	30	20	29
17.09.76-28.09.76	31	20	11
28.09.76-19.10.76	32	20	21
19.10.76-28.10.76	33	20	09
28.10.76-11.11.76	34	20	14
11.11.76-25.11.76	35	20	14
25.11.76-09.12.76	36	20	14
09.12.76-23.12.76	37	20	14
23.12.76-07.01.77	38	20	14
07.01.77-21.01.77	39	10	14
21.01.77-04.02.77	40	10	14
04.02.77-18.02.77	41	10	14

PÉRIODE	S	PT	D
18.02.77-04.03.77	42	10	14
04.03.77-18.03.77	43	10	14
18.03.77-01.04.77	44	10	14
01.04.77-21.04.77	45	10	20
21.04.77-18.05.77	46	10	27
18.05.77-15.06.77	47	10	28
15.06.77-01.07.77	48	10	16
01.07.77-18.07.77	49	10	17
18.07.77-28.07.77	50	10	10
28.07.77-05.09.77	51	10	39
05.09.77-20.09.77	52	09	15
20.09.77-04.10.77	53	10	14
04.10.77-18.10.77	54	10	14
18.10.77-02.11.77	55	10	15
02.11.77-16.11.77	56	10	14
16.11.77-02.12.77	57	10	16
02.12.77-14.12.77	58	10	12
14.12.77-23.12.77	59	10	09
23.12.77-06.01.78	60	10	14
06.01.78-20.01.78	61	10	14
20.01.78-03.02.78	62	10	14
03.02.78-17.02.78	63	10	14
17.02.78-17.03.78	64	10	28
17.03.78-31.03.78	65	10	14
31.03.78-11.04.78	66	10	11
11.04.78-24.04.78	67	10	13
24.04.78-09.05.78	68	10	15
09.05.78-25.05.78	69	10	16
25.05.78-06.06.78	70	10	12
06.06.78-20.06.78	71	10	14
20.06.78-04.07.78	72	10	14
04.07.78-19.07.78	73	10	15
19.07.78-05.09.78	74	10	48
05.09.78-19.09.78	75	10	14
19.09.78-03.10.78	76	10	14
03.10.78-19.10.78	77	10	16
19.10.78-31.10.78	78	10	12
31.10.78-14.11.78	79	10	14
14.11.78-06.12.78	80	10	22
06.12.78-19.12.78	81	10	13
-------	-----	-----	-----

Source : MNHN, Paris

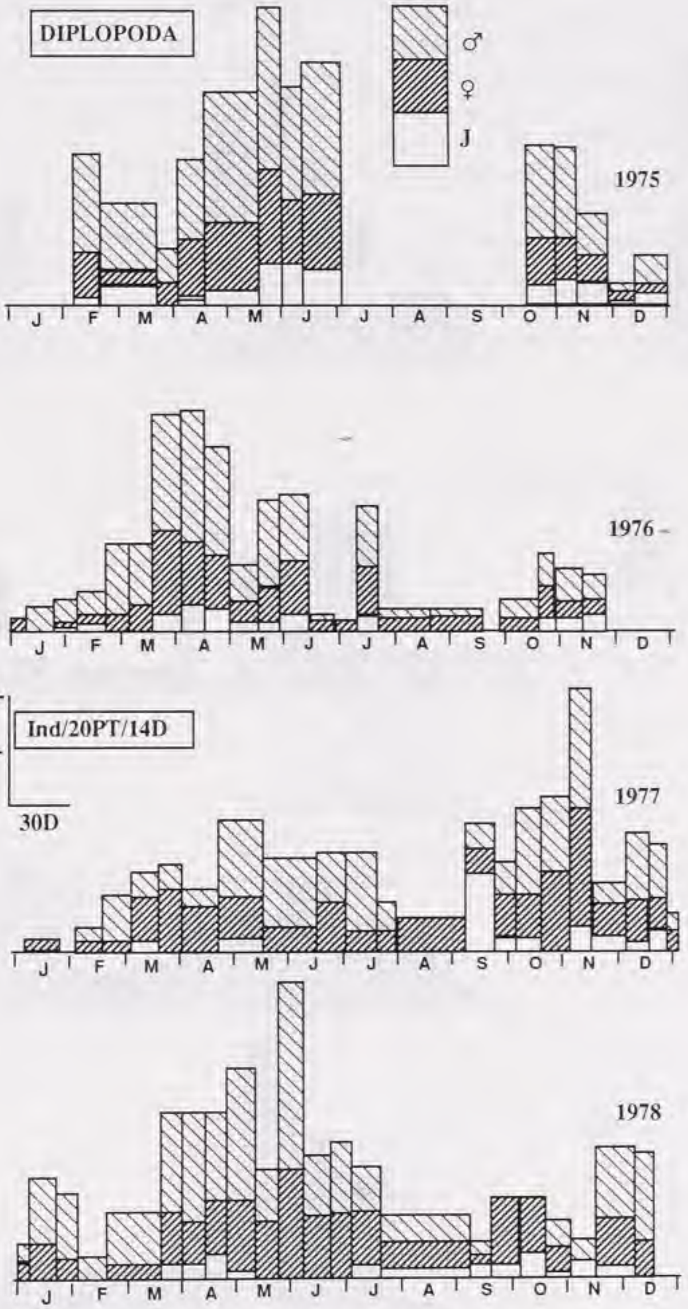


FIG. 2. — Cycles d'activité de l'ensemble du peuplement de diplopodes dans les couches supérieures du sol, de février 1975 à décembre 1978 (fractions mâle, femelle et juvénile de la communauté).

FIG. 2. — Activity cycles of the whole millipede community in the upper soil layers of the temperate Foljuif forest, from February 1975 to December 1978 (male, female and juvenile parts of the community).

Source : MNHN, Paris

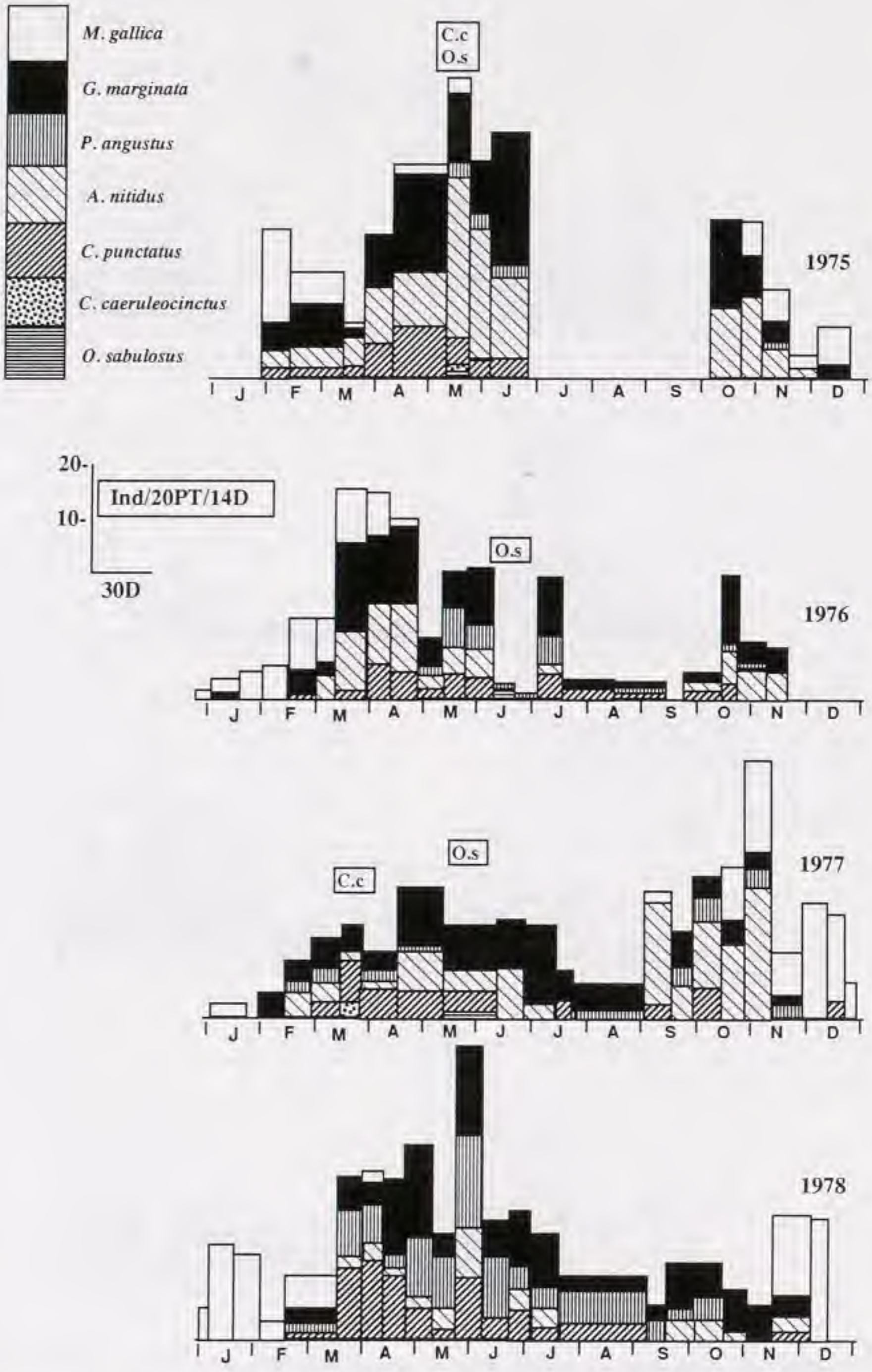


FIG. 3. — Cycles d'activité des sept espèces dominantes de diplopodes dans les couches supérieures du sol, de février 1975 à décembre 1978 (total des individus capturés dans les pièges).

FIG. 3. — Activity cycles of the seven mainly representative millipede species (total trapped individuals for each species) in the upper soil layers of the temperate Foljuif forest, from February 1975 to December 1978.

Source : MNHN, Paris

Melogona gallica

Une activité de surface du chordeumide *Melogona gallica* (= *Microchordeuma gallicum* auct.) est mise en évidence uniquement pendant l'hiver, de la fin d'octobre au début d'avril. Les individus capturés sont en grande majorité des adultes (stade IX) parmi lesquels on note une dominance relative fréquente des mâles. Les juvéniles, rares dans les pièges, sont représentés par des individus subadultes appartenant aux stades VII et VIII. Tous les Chordeumatida ont une durée de vie courte et un cycle biologique établi sur 1 ou 2 ans (BLOWER, 1978, 1979 ; PEDROLI-CHRISTEN, 1978 ; MEYER, 1979 ; DAVID, 1984). A Foljuif, le cycle de *M. gallica* est annuel et la période d'activité des adultes est en totale correspondance avec leur maximum d'abondance à la limite des couches F et H. En revanche, le maximum de densité observé à la fin du printemps à partir de relevés quantitatifs (GEOFFROY, 1985) correspond à une grande quantité de juvéniles qui ne montrent pas d'activité de déplacement dans les couches de surface. L'absence totale de capture durant l'hiver 76-77 traduit l'effet immédiat de la sécheresse de 1976 sur la population (Fig. 4).

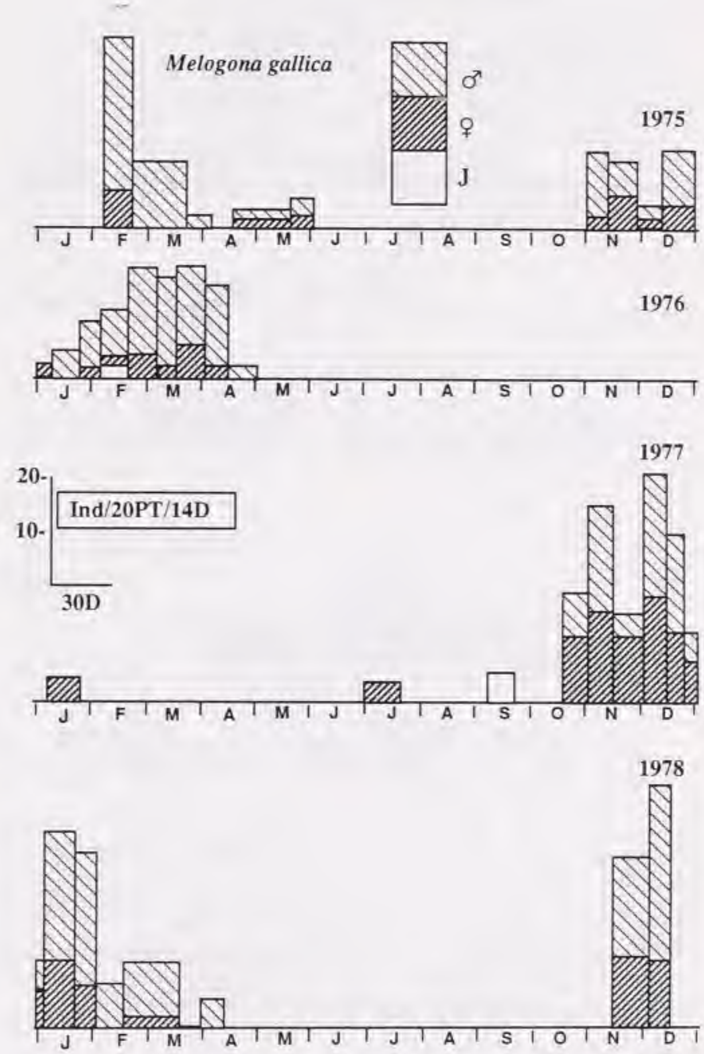


FIG. 4. — Cycles d'activité de *Melogona gallica* (Chordeumatida) dans les couches supérieures du sol, de février 1975 à décembre 1978.

FIG. 4. — Activity cycles of the species Melogona gallica *(Chordeumatida) in the upper soil layers of the temperate Foljuif forest, from February 1975 to December 1978.*

Source : MNHN, Paris

Polydesmus angustus

P. angustus est une espèce relativement peu abondante dans le site étudié, où elle effectue son cycle biologique soit en un an, soit en deux ans, selon les individus. Les périodes de pontes sont très étalées dans le temps, ce qui peut être reflété par la longue période d'activité de surface des adultes (stade VIII), notamment des femelles. Le cycle de 1978 en est particulièrement caractéristique (février à septembre), le maximum de mai-juin pouvant correspondre à la maturation des femelles (cf. COURET, 1985). La fraction juvénile piégée est représentée par des subadultes appartenant aux stades VI et VII. On les capture essentiellement en automne (septembre à novembre). Ils correspondent à une partie de la population hivernale qui deviendra adulte au printemps suivant. La fraction immature de la population (stades II à V), présente dans les couches profondes de la litière et du sol en été, n'est pas capturée par un système de piégeage visant à sélectionner les individus actifs en surface (BLOWER, 1970). Cela n'empêche ni l'activité, ni la mobilité à plus grande profondeur (COURET, 1985).

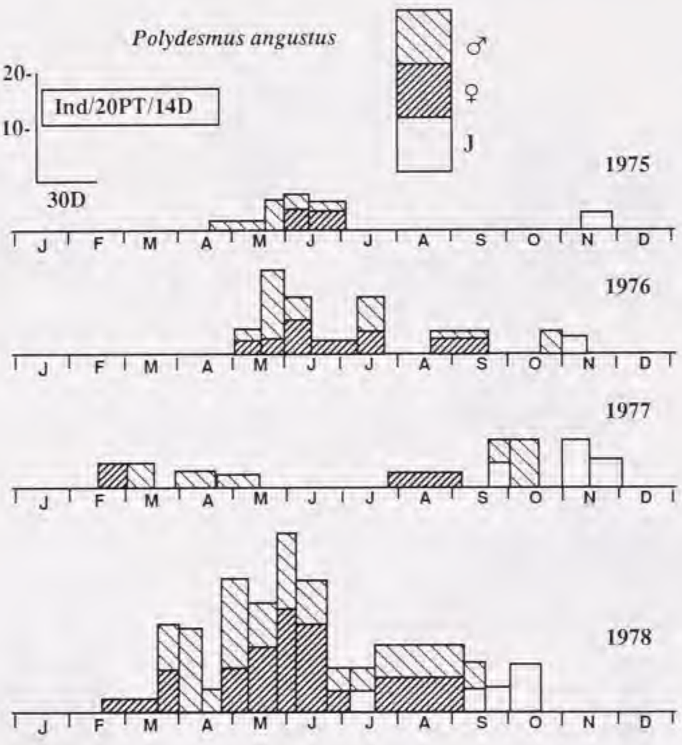


FIG. 5. — Cycles d'activité du Polydesmida *Polydesmus angustus* dans les couches supérieures du sol, de février 1975 à décembre 1978.

FIG. 5. — Activity cycles of the Polydesmid species Polydesmus angustus *in the upper soil layers of the temperate Foljuif forest, from February 1975 to December 1978.*

L'activité des adultes est surtout marquée par un pic de printemps pour les deux sexes avec un maximum en mai-juin. En automne en revanche, un très léger pic ne concerne, certaines années, que les mâles (octobre). Le maximum de printemps s'accorde bien avec les résultats obtenus par divers auteurs (BANERJEE, 1967a ; HAACKER, 1968 ; BLOWER, 1970 ; COURET, 1985). Par ailleurs, on observe une importance relative plus grande des mâles au début de la période d'activité (mars à mai). Cependant, ce phénomène ne dure pas et le reste de la période active montre un équilibre entre les sexes ou au contraire, une plus forte présence des femelles en mai-juin (Fig. 5).

En dépit de toute preuve formelle liant l'activité de surface des adultes aux périodes de reproduction, on est tenté de conserver cette interprétation pour la période active de printemps

Source : MNHN, Paris

chez *P. angustus*. Nous devons garder à l'esprit que les femelles matures de *P. angustus* sont capables d'effectuer plusieurs ovipositions ± étalées dans le temps au cours de leur vie adulte (SNIDER, 1981 ; DAVID & CÉLÉRIER, 1993) et que les modalités de la copulation elles-mêmes peuvent présenter de très larges variations (VERHOEFF, 1928 ; HUSSON, 1937 ; SAHLI, 1969). Ces caractéristiques de la biologie de l'espèce, liées à une activité prolongée des adultes (BLOWER, 1969 ; BANERJEE, 1973) sont confirmées par l'observation d'accouplement et de pontes à Foljuif s'étendant de début avril à la fin novembre. Le nombre d'oeufs trouvés dans les logettes de pontes est variable, allant de 160 à 658 (!) pour une même logette et reflète la capacité potentielle des femelles à réaliser 1 à 4 pontes successives au cours de l'année. La période de mobilité maximum est suivie d'une disparition progressive des adultes actifs que l'on peut lier d'une part à la mortalité des mâles et des femelles après la reproduction, d'autre part aux modifications du climat à l'approche de l'hiver durant lequel les subadultes et adultes survivants migrent dans les couches profondes de l'humus et dans les bois morts (GEOFFROY, 1985).

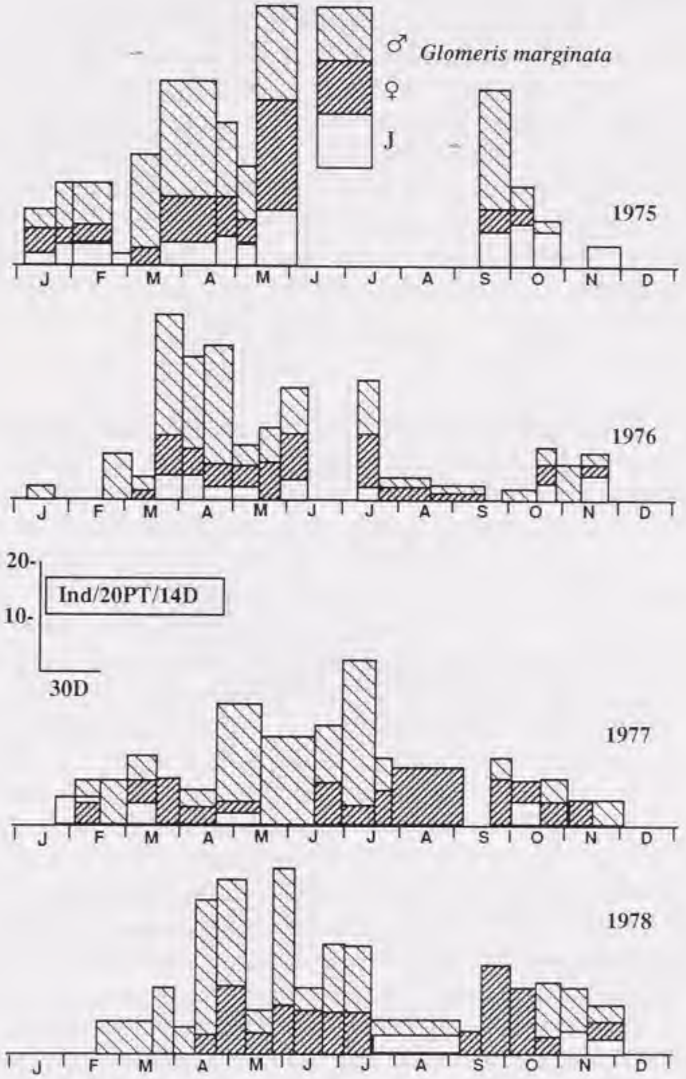


FIG. 6. — Cycles d'activité du Glomerida *Glomeris marginata* dans les couches supérieures du sol, de février 1975 à décembre 1978.

FIG. 6. — Activity cycles of the Glomerid species Glomeris marginata *in the upper soil layers of the temperate Foljuif forest, from February 1975 to December 1978.*

Source : MNHN, Paris

Glomeris marginata

Espèce à longue durée de vie (jusqu'à 14 ans selon HEATH *et al.*, 1974), *Glomeris marginata* présente une activité de surface plus ou moins importante tout le long de l'année. Elle est presque exclusivement le fait des stades adultes épimorphes mâles et femelles. Le rapport des sexes est le plus souvent très en faveur des mâles, notamment durant la période d'activité maximale qui s'étend de mars à juillet (Fig. 6). On observe durant cette période une diminution de l'abondance relative des mâles piégés par rapport aux femelles qui dominent au début de l'été et au début de l'automne, ce qui s'accorde avec les observations de HEATH *et al.* (1974). Le pic automnal est moins marqué que celui du printemps. C'est à l'automne (septembre à novembre) que la proportion de juvéniles dans les pièges est la plus élevée. Il s'agit d'individus appartenant soit aux stades épimorphes immatures (VI, ...?), soit au dernier stade anamorphe, stade V (BOCOCK *et al.*, 1967).

La position des pics d'activité des adultes au cours du cycle annuel est en correspondance avec celui des pics des densités de la fraction épimorphe de la population (BLOWER & GABBUT, 1964). Le pic de densité des immatures que l'on observe fréquemment au printemps n'apparaît pas ici. Leur niveau d'activité et de déplacement se situe dans les couches inférieures de l'humus. Seuls les derniers stades subadultes sont piégés.

Selon BOCOCK & HEATH (1967), les périodes d'inactivité de *G. marginata* dans les couches de litière correspondent au moment de l'année ou la température de surface est basse (<6°C) et au moment de la mue. Dans la forêt de Foljuif, l'inactivité hivernale s'étend de décembre à février et la période estivale de mue des adultes est ponctuelle (3 à 4 semaines en juillet-août le plus souvent). Cela nous conduit à une durée annuelle d'activité de surface de 275 jours (3/4 de l'année) supérieure à celle rapportée par CARREL (1984) pour les forêts d'Angleterre. Cette durée d'activité peut même être bien supérieure dans le cas d'années à hivers doux.

Cylindroiulus punctatus

L'activité de surface de ce Julida est principalement marquée par un pic au printemps (de mars à juin) et diminue progressivement durant l'été. En revanche, durant l'automne, les captures demeurent faibles ou nulles, l'activité reprend régulièrement dès la fin de l'hiver suivant (Fig. 7). Les adultes mâles et femelles (stades VII à XII) représentent la quasi-totalité des individus piégés, les immatures sont constitués d'individus appartenant aux stades V et VI. Le rapport entre les sexes est extrêmement variable d'une année sur l'autre et difficilement interprétable. Très favorable aux mâles adultes en 1975 et 1976, le sex-ratio montre au contraire une forte importance des femelles en 1977 et un état proche de l'équilibre en 1978. Cela montre, une fois de plus, combien l'interprétation des cycles d'activité est délicate et comme il est facile de privilégier une hypothèse (*e.g.* l'activité des mâles adultes lié à l'accouplement) au détriment d'une autre en observant un seul cycle annuel. La diminution du niveau d'activité observée en 1976 et 1977 peut être mise en relation avec les conditions climatiques caractérisant l'année 1976. En 1978, le taux de capture saisonnier devient supérieur à celui de 1975, ce qui peut s'expliquer par un accroissement global de l'activité de la population au cours des années. Le pic d'activité unique au printemps semble bien être une caractéristique constante de l'espèce. BANERJEE (1967a) constate un maximum d'activité en avril-mai suivi d'une décroissance régulière jusqu'en décembre alors que DRIFT (1951) signale une période d'activité exclusivement de début-avril à la mi-mai.

L'activité de surface printannière a lieu au moment où la population de *C. punctatus* de la forêt de Foljuif présente une abondance relative importante par rapport aux autres diplopodes (GEOFFROY, 1981a). Elle coïncide avec un pic de densité observé à la même période dans les couches supérieures L+F, suivi d'une migration d'une grande partie de la population dans les bois morts tombés au sol dès le début de l'été (BANERJEE, 1967b ; GEOFFROY, 1985). Le pic

Source : MNHN, Paris

de densité, observé à la fois chez les adultes et les juvéniles au printemps, concorde avec une importante activité de surface. En revanche, le pic de densité des adultes signalé en automne (GEOFFROY, 1981b) correspond à une période de migration en direction des couches organo-minérales du sol (H+A1), ce qui explique en partie l'absence de capture par les pièges à cette saison. De même, les fortes densités observées de juillet à novembre par BLOWER & GABBUT (1964), qui sont en grande partie dues à des stades juvéniles successifs, ne semblent pas avoir de répercussions sur une activité de surface des individus en dehors de la période printannière. La relation étroite que présente cette espèce avec les bois morts en décomposition lors des périodes de mue et de reproduction joue un rôle capital dans l'interprétation de son cycle d'activité de surface (GEOFFROY, 1981b).

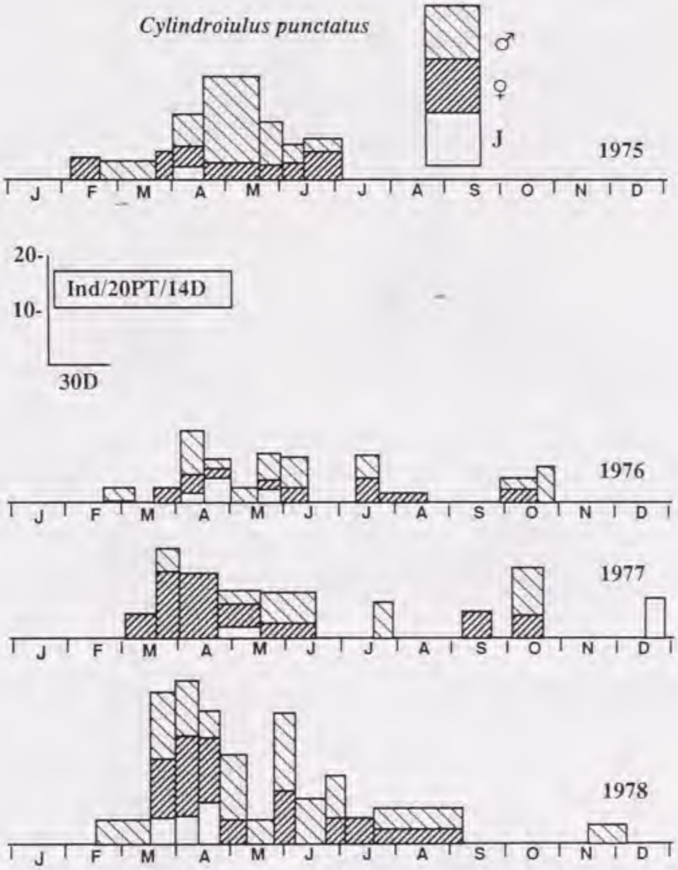


FIG. 7. — Cycles d'activité du Julida *Cylindroiulus punctatus* dans les couches supérieures du sol, de février 1975 à décembre 1978.

FIG. 7. — Activity cycles of the Julid species Cylindroiulus punctatus *in the upper soil layers of the temperate Foljuif forest, from February 1975 to December 1978.*

Allajulus nitidus

Contrairement à *C. punctatus*, *Allajulus nitidus* (appelé *Cylindroiulus nitidus* dans les travaux antérieurs de nombreux auteurs) présente manifestement deux pics d'activité de surface au cours du cycle annuel : le premier au printemps, de mars à juin, et le second en automne, de septembre à novembre. Ce phénomène se répète régulièrement chaque année. L'été et l'hiver sont caractérisés par un arrêt total de l'activité de surface. Les individus capturés sont essentiellement des adultes mâles (stades VII à IX) et femelles (stades VIII à XI). Les juvéniles, peu fréquents et peu nombreux, sont représentés par des subadultes des stades VI et VII.

On ne remarque aucun décalage évident entre les périodes d'activité des mâles et des femelles, les deux sexes étant largement représentés lors des deux périodes d'activité maximale.

Source : MNHN, Paris

On note toutefois une prépondérance des femelles durant le printemps 1976 et l'automne 1978. Un cycle d'activité proche de celui-ci existe dans d'autres populations forestières de *A. nitidus* (e.g. DAVID, 1982, en forêt d'Orléans). Des différences portent cependant sur le décalage temporel ou l'activité relative observés entre les sexes. L'activité des femelles adultes domine au printemps et est précoce en automne en forêt d'Orléans, alors que l'activité relative des mâles est plus fréquente et plus durable dans la population de Foljuif, à l'exception de l'automne 1978. Il convient toutefois de rappeler que l'interprétation biologique de ces taux de captures est délicate et que plusieurs causes sont à l'origine des variations saisonnières inter-annuelles et inter-populations.

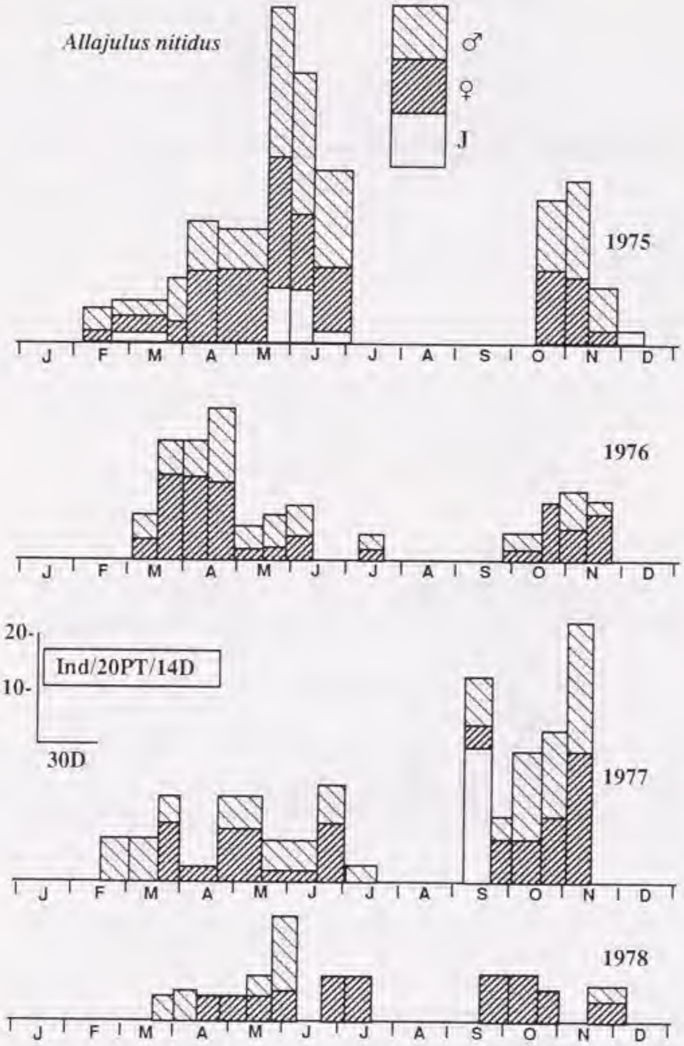


FIG. 8. — Cycles d'activité du Julida *Allajulus nitidus* dans les couches supérieures du sol, de février 1975 à décembre 1978.

FIG. 8. — Activity cycles of the Julid species Allajulus nitidus *in the upper soil layers of the temperate Foljuif forest, from February 1975 to December 1978.*

A. nitidus est une espèce très abondante dans certains écosystèmes forestiers (BLOWER, 1979 ; BLOWER & MILLER, 1977), le maximum d'activité coïncide alors avec le maximum de densité au printemps et en automne (GEOFFROY, 1981b ; DAVID, 1982). A Foljuif, durant la période d'étude considérée ici, *A. nitidus* domine numériquement le peuplement de diplopodes de la litière toute l'année sauf une partie de l'hiver (GEOFFROY, 1981a). On ne peut exclure

Source : MNHN, Paris

qu'une augmentation de l'activité soit en partie liée à la reproduction : à l'accouplement d'une part, traduit par l'activité intense des mâles adultes, à la ponte d'autre part lors de l'activité maximale et dominante des femelles au printemps. C'est l'interprétation la plus couramment admise par les auteurs étudiant l'activité de diplopodes julides (*e.g.* BANERJEE, 1967b ; COTTON & MILLER, 1974). Nous devons considérer aussi que les périodes de forte activité des adultes sont liées aux conditions climatiques qui favorisent la dispersion de la population dans l'ensemble des couches de la litière, notamment au début de l'automne, où elle coexiste temporairement avec *C. punctatus* (GEOFFROY, 1985). Les variations inter-annuelles ne concernent ni le rythme ni la nature du cycle saisonnier d'activité. En revanche, on constate une diminution progressive du niveau d'activité, qui se traduit par un taux de capture de printemps décroissant régulièrement de 1975 à 1978. La diminution observée en automne 1976 et au printemps 1977 s'interprète comme une réaction immédiate aux conditions de sécheresse de 1976. Cet effet n'est pas durable puisque l'activité reprend fortement à l'automne de 1977. Pourtant, le cycle de 1978 est caractérisé par un niveau d'activité plus faible, contrairement à toutes les espèces étudiées précédemment. Cela induit un changement dans l'organisation fonctionnelle du peuplement que l'on doit considérer en comparant les variations relatives de populations proches, notamment celles des autres Julida.

DISCUSSION

Considéré dans son ensemble, le peuplement de diplopodes édaphiques de la forêt de Foljuif présente constamment une activité de surface dans la litière. Le cycle annuel, d'allure “bimodale”, montre un premier pic au printemps et un second pic à l'automne. Ceci est la résultante de l'activité de la fraction adulte et subadulte de plusieurs populations dont l'importance relative varie considérablement au cours du temps. *Glomeris marginata* et *Polydesmus angustus* assurent, à des degrés divers, un apport constant d'individus actifs tout au long du cycle annuel. L'activité hivernale est essentiellement due au chordeumide *Melogona gallica*. Les pics printaniers et automnaux sont accentués par l'activité conjuguée des julides, surtout au printemps pour *Cylindroiulus punctatus*, et reflète en grande partie le cycle d'activité de la population la plus abondante lors des premières années de la période d'étude : *Allajulus nitidus*.

Les traits généraux du cycle annuel d'activité ainsi défini se répètent régulièrement chaque année. La réponse à court terme due aux effets du climat local dans l'écosystème ne s'étend pas au-delà du cycle suivant. Ainsi, l'impact de la sécheresse du printemps et de l'été de 1976 se fait-il sentir de l'automne 1976 à la fin du printemps 1977.

Au-delà de ce constat général de relatives stabilité et régularité, des modifications dans la composition du peuplement apparaissent au cours du temps, sur lesquelles il y a lieu de s'interroger. Elles concernent notamment l'importance relative des deux espèces de Julida les plus fréquemment capturées dans les pièges : *A. nitidus* et *C. punctatus* (FIG. 9). *A. nitidus* domine clairement le peuplement de diplopodes en 1975 et il conserve une importance relative considérable jusqu'en automne 1977. Mais l'observation des quatre cycles successifs montre une diminution progressive de cette espèce durant la phase de printemps, au profit de *C. punctatus* qui finit par le remplacer en grande partie en 1978. *A. nitidus* reste dominant durant le début de l'automne, les grands individus de *C. punctatus* étant alors encore distribués dans les bois morts, ce qui explique le fort pourcentage que représente *A. nitidus* dans les dernières séries de piégeage (FIG. 10). Cette diminution considérable de *A. nitidus* pourrait n'être en fait qu'un phénomène temporaire dû aux conditions locales autorisant les captures ou, partiellement, au hasard des déplacements. Il semble que la modification constatée ait une signification plus profonde et plus durable. Il ne s'agit pas seulement d'une diminution de l'activité mais également de l'abondance relative, mesurée par la densité des individus dans les échantillonnages quantitatifs. En outre, les études ultérieures confirment bien cette tendance.

Source : MNHN, Paris

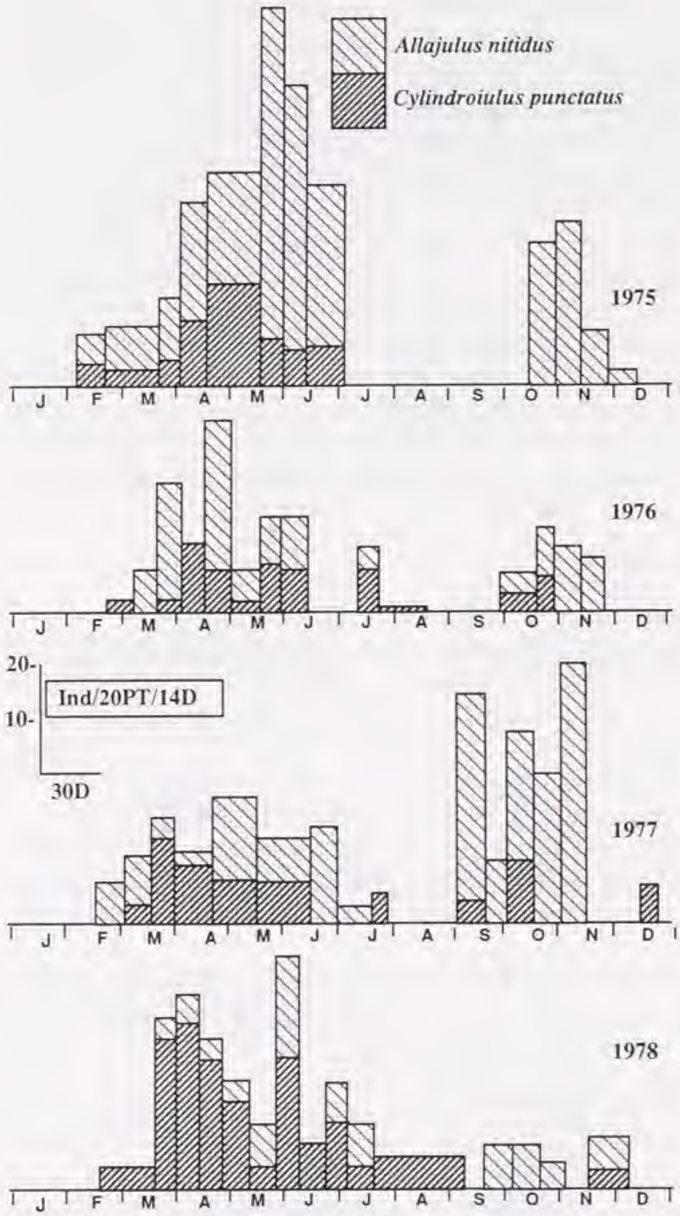


FIG. 9. — Cycles d'activité comparés de deux espèces de Julides, *Allajulus nitidus* (An) et *Cylindroiulus punctatus* (Cp), dans les couches supérieures du sol, de février 1975 à décembre 1978 (nombre total d'individus pour chaque population).

FIG. 9. — Compared activity cycles of two Julid species, Allajulus nitidus *(An) and* Cylindroiulus punctatus *(Cp), in the upper soil layers of the temperate Foljuif forest, from February 1975 to December 1978 (total number of individuals for each specific population).*

Durant le cycle annuel 1976, *A. nitidus* apparaît nettement comme le diplopode le plus abondant du peuplement, tant en densité qu'en biomasse (GEOFFROY, 1981a). Il domine largement *C. punctatus* dans les couches de litière, ainsi que le montrent les modalités de la coexistence de ces deux populations dans l'écosystème (GEOFFROY, 1981b). Au cours du cycle annuel de 1982 au contraire, on observe un accroissement relatif et une dominance de *C. punctatus* par rapport à *A. nitidus* et par rapport aux autres diplopodes durant toutes les phases saisonnières de l'année (GEOFFROY, 1985).

En première analyse, les variations relatives observées entre les deux populations tout au long de la période de piégeage sont considérées comme un phénomène traduisant une réelle

Source : MNHN, Paris

modification de l'activité de l'une par rapport à l'autre et un remplacement progressif, dans les couches L+F de la litière, de *A. nitidus* par *C. punctatus* (Fig. 10). La réalité de ce phénomène doit être vérifiée par l'analyse comparative des cycles d'abondance des deux espèces au cours de l'étude à long terme qui a suivi la période de piégeage (BLANDIN *et al.*, 1985) et au cours de laquelle l'importance relative de *C. punctatus* semble se confirmer (GEOFFROY, *in prep.*). Cela présente un intérêt majeur dans la dynamique de l'organisation et des modalités d'action d'un groupe fonctionnel de macroarthropodes saprophages consommateurs et transformateurs des couches supérieures peu dégradées de la litière, au cours des deux premières années de décomposition de celle-ci.

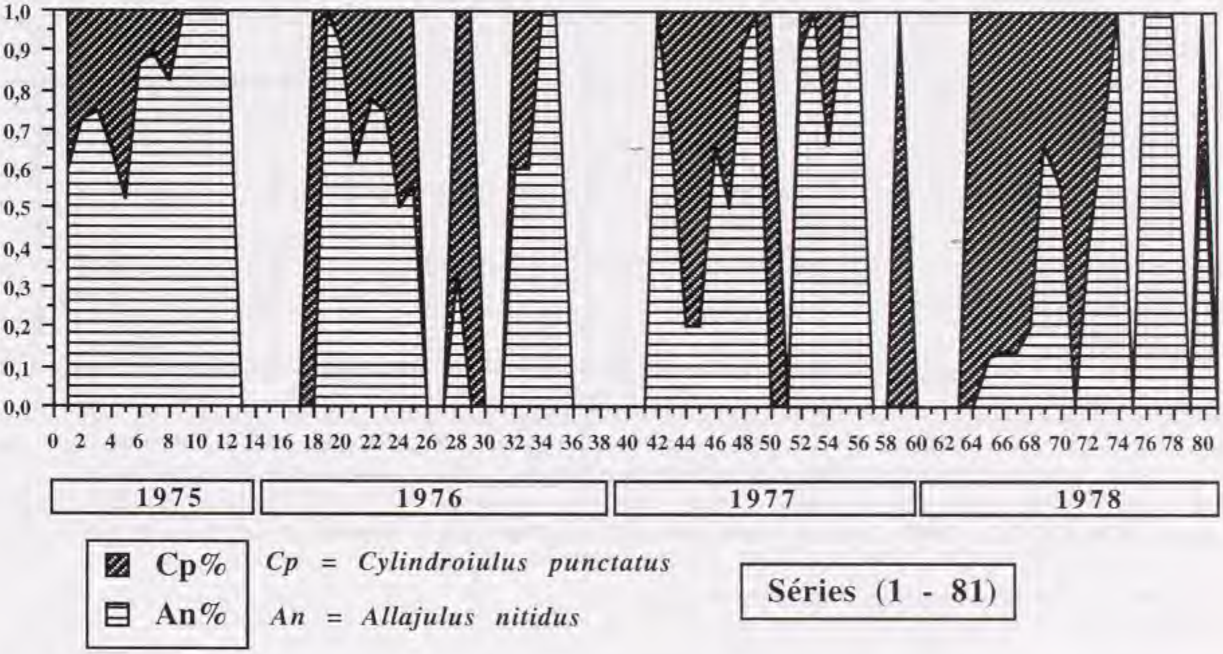


FIG. 10. — Importance relative de deux espèces de Julides, *Allajulus nitidus* (An) et *Cylindroiulus punctatus* (Cp), durant la période de piégeage (séries 1 à 81), dans les couches supérieures du sol de la forêt de Foljuif.

FIG. 10. — Relative importance of two Julid millipedes, Allajulus nitidus *(An) and* Cylindroiulus punctatus *(Cp), during the trapping period (series 1 to 81) in the upper soil layers of the temperate Foljuif forest.*

A l'échelle de l'ensemble des compartiments de litière et des horizons du sol, c'est la totalité de la guilde des diplopodes saprophages qui entre en jeu, depuis les plus jeunes stades jusqu'aux adultes à mues post-imaginales. Mais toutes les catégories d'individus n'agissent pas en même temps et de la même façon à l'intérieur d'un même compartiment édaphique. La sélection d'une partie du peuplement lors de la capture par piégeage nous renseigne sur la nature des individus capables d'agir au sein des couches les plus superficielles de la litière. Elle contribue à distinguer, parmi les diplopodes, deux groupes d'animaux montrant des modalités d'activité et de fonction différentes dans les divers compartiments édaphiques de l'écosystème. Seuls les individus les plus grands - et donc les plus âgés - semblent capables de se mouvoir dans les couches les moins profondes de la litière, et d'y réaliser une fonction de consommation et de transformation. Ainsi que l'on distingue couramment "micro-arthropodes" et "macro-arthropodes", il conviendrait de distinguer des "micro-diplopodes" et des "macro-diplopodes". Ces deux groupes sont séparés ici par une limite liée au taux de capture potentiel dans nos pièges

Source : MNHN, Paris

d'interception qui sélectionnent préférentiellement les individus qui se déplacent activement en surface. Une limite approximative est ainsi définie au sein de l'ensemble des diplopodes. Les macro-diplopodes, fréquents dans les pièges, représentent un groupe fonctionnel particulier (Fig. 11). Bien entendu, l'organisation d'un tel groupement d'individus doit être confirmée par d'autres voies d'observation et d'expérimentation : répartition spatio-temporelle des individus et modalités de la consommation des feuilles. En outre, la comparaison et l'intégration de ces mesures à celles obtenues chez les isopodes oniscoïdes devraient favoriser la compréhension d'un "groupe fonctionnel de macroarthropodes saprophages" dans l'écosystème forestier étudié.

STADIA	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Melogona gallica	⊙	⊙	⊙	⊙	⊙	⊙	*	*	*	-	-	-
Polydesmus angustus	⊙	⊙	⊙	⊙	⊙	*	*	*	-	-	-	-
Glomeris marginata	⊙	⊙	⊙	⊙	*	*	*	*	*	*	*	*
Allajulus nitidus	⊙	⊙	⊙	⊙	⊙	*	*	*	*	*	*	*
Cylindroiulus punctatus	⊙	⊙	⊙	⊙	⊙	*	*	*	*	*	*	*
Cylindroiulus caeruleocinctus	⊙	⊙	⊙	⊙	⊙	⊙	⊙	*	*	*	*	*
Ommatoiulus sabulosus	⊙	⊙	⊙	⊙	⊙	*	*	*	*	*	*	*

FIG. 11. — Répartition des différents stades de sept espèces de diplopodes dans les couches supérieurs de litière et de sol de la forêt tempérée de Foljuif : individus capturés par piégeage d'interception de février 1975 à décembre 1978. Ligne en gras : peuplement actif de macro-diplopodes ; ligne double : peuplement de micro-diplopodes.

FIG. 11. — Occurence of the different stadia of seven millipede species in the upper soil and litter layers of the temperate Foljuif forest: individuals caught in Pitfall traps from February 1975 to December 1978. Thick line: active macro-diplopod community; double line: micro-diplopod community.

* : Frequent or abundant. ⊙ : Occasional or scarce.

REMERCIEMENTS

Ce travail a bénéficié d'une aide du Ministère des Universités et du Ministère de l'Enseignement Supérieur et de la Recherche. Nous sommes reconnaissants à M. le Pr. P. BLANDIN (M.N.H.N., Brunoy) pour l'attention soutenue qu'il a apportée à l'élaboration de cette publication. Nous remercions M. LOYAU et Mme RAULO (E.N.S., Station Biologique de Foljuif) pour leur aide technique sur le terrain et au laboratoire.

RÉFÉRENCES

ADIS, J., 1979. — Problems of interpreting arthropod sampling with pitfall traps. *Zool. Anz.*, **202** : 177-184.

ALBERT, M., 1978. — Bodenfallenfänge von Diplopoden und Isopoden in Wüppertaler Wäldern (MB 4708/09). *Jahr. Naturw. V. Wuppertal*, **31** : 46-49.

BAKER, G. H., 1979. — The activity patterns of *Ommatoiulus moreletti* (Diplopoda: Julidae) in South Australia. *J. Zool. Lond.*, **188** : 173-183.

BAKER, G. H., 1985. — The distribution and abundance of the Portuguese millipede *Ommatoiulus moreleti* (Diplopoda: Julidae) in Australia. *Aust. J. Ecol.*, **10** : 249-259.

BAKER, G. H., 1988. — Patterns in the activity of the millipede *Ommatoiulus moreleti* (Diplopoda: Iulidae). *Aust. Entomol. Mag.*, **15** : 127-139.

BANERJEE, B., 1967a. — Diurnal and seasonal variations in the activity of the millipedes *Cylindroiulus punctatus* (Leach), *Tachypodoiulus niger* (Leach) and *Polydesmus angustus* Latzel. *Oikos*, **18** : 141-144.

BANERJEE, B., 1967b. — Seasonal changes in the distribution of the millipede *Cylindroiulus punctatus* (Leach) in decaying logs and soil. *J. Anim. Ecol.*, **36** : 171-177.

Source : MNHN, Paris

BANERJEE, B., 1970. — A mathematical model on sampling diplopods using pitfall traps. *Oecologia*, **4** : 102-105.

BANERJEE, B., 1973. — The breeding biology of *Polydesmus angustus* Latzel (Diplopoda, Polydesmidae). *Nork. ent. Tidsskr.*, **20** : 291-294.

BARBER, H., 1931. — Traps for cave-inhabiting insects. *J. Elisha Mitchell sci. Soc.*, **46** : 259-266.

BARLOW, A., 1957. — A factorial analysis of distribution in three species of Diplopods. *Tijdschr. Ent.*, **100** : 349-426.

BARLOW, C. A., 1958. — Distribution and seasonal activity in three species of diplopods. *Arch. Neerland. Zool.*, **13** : 108-133.

BLANDIN, P., ABBADIE, L., COURAULT, S., GARAY, I., & GEOFFROY, J. J., 1980. — Etude d'un écosystème forestier mixte. I. Climat, structure de la végétation et retombées de litière. *Rev. Ecol. Biol. Sol*, **17** : 181-198.

BLANDIN, P., FLOGAITIS, E., ARBEILLE, J., & GEOFFROY., J. J., 1985. — Les variations interannuelles de macroarthropodes édaphiques dans une forêt tempérée. *Bull. Ecol.*, **16** : 273-283.

BLOWER, J. G., 1969. — Age structure of millipede populations in relation to activity and dispersion. *In* : J. G. SHEALS, *The soil ecosystem.*. London, Publ. Syst. Ass., **8** : 209-216.

BLOWER, J. G., 1970. — The millipedes of a Cheshire wood. *J. Zool. Lond.*, **160** : 455-496.

BLOWER, J. G., 1978. — Anamorphosis in the Nematophora. *Abh. Verh. naturwiss. Ver. Hamburg*, **21/22** : 97-103.

BLOWER, J. G., 1979. — The millipede faunas of two British limestone woods. *In* : M. CAMATINI, *Myriapod Biology*. London, Academic Press : 203-214.

BLOWER, J. G. & GABBUT., P. D., 1964. — Studies on the millipedes of a Devon oak wood. *Proc. Zool. Soc. London*, **143** : 143-176.

BLOWER, J. G. & MILLER., P. F., 1977. — The life-history of the Julid millipede *Cylindroiulus nitidus* in a Derbyshire wood. *J. Zool. Lond.*, **183** : 339-351.

BOCOCK, K. L. & J. HEATH., 1967. — Feeding activity of the millipede *Glomeris marginata* (Villers) in relation to its vertical distribution in the soil. *In* : O. GRAF & J. E. SATCHELL, *Progress in Soil Biology*. Amsterdam, North Holland Publ. C° : 233-240.

BOCOCK, K. L., M. D., MOUNTFORD & HEATH., J., 1967. — Estimation of annual production of a millipede population. *In* : K. PETRUSEWICZ, *Secondary productivity of terrestrial ecosystems*. Warsawa : 727-739.

BRIGGS, J. B., 1961. — A comparison of pitfall trapping and soil sampling in assessing populations of two species of ground beetles. *Rep. E. Malling Res. Sta.*, **1960** : 108-112.

CARREL, J. E., 1984. — Defensive secretion of the pill millipede *Glomeris marginata*. I. Fluid production and storage. *J. Chem. Ecol.*, **10** : 44-51.

COTTON, M. J. & MILLER, P. F., 1974. — A population of *Cylindroiulus latestriatus* (Curtis) in sand dunes. *Symp. Zool. Soc. London*, **32** : 589-602.

COURET, T., 1985. — Recherches sur la biologie et l'écologie de deux populations de diplopodes en forêt d'Orléans : *Polyzonium germanicum* Brandt, 1831 et *Polydesmus angustus* Latzel, 1884. Thèse, Doctorat de 3e cycle, Ecologie, Orléans, 144 pp.

DAVID, J. F., 1982. — Variabilité dans l'espace et dans le temps des cycles de vie de deux populations de *Cylindroiulus nitidus* (Verhoeff) (Julida). *Rev. Ecol. Biol. Sol*, **19** : 411-425.

DAVID, J. F., 1983. — Contribution à l'étude des populations de Diplopodes en Forêt d'Orléans, et de leur rôle dans la dégradation de la litière. Thèse, Doctorat de 3e cycle, Ecologie, Orléans, 149 pp.

DAVID, J. F., 1984. — Le cycle annuel du diplopode *Microchordeuma gallicum* (Latzel, 1884). *Bull. Soc. zool. France*, **109** : 61-70.

DAVID, J. F. & CÉLÉRIER., M. L., 1993. — Nombre d'ovipositions et fécondité chez le Diplopode *Polydesmus angustus* Latzel (Polydesmida : Polydesmidae). *C. R. Acad. Sci. Paris*, **316** : 225-228.

DAVID, J. F.& POUSSARDIN, C., 1983. — L'interprétation du piégeage du Diplopode *Microchordeuma gallicum* (Latzel, 1884). *Rev. Ecol. Biol. Sol*, **20** : 579-587.

DETHIER, M. & PEDROLI-CHRISTEN., A., 1983. — Diplopodes et Chilopodes d'une pelouse alpine du Parc National Suisse. *Bull. Soc. Vaudoise Sci. nat.*, **364** : 373-379.

DRACH, A., BENEST G. & CANCELA DA FONSECA, J. P., 1981. — Analyse comparative de différents types de pièges basée sur l'étude de deux peuplements de Carabiques (Col. Carabidae). *Rev. Ecol. Biol. Sol*, **18** : 91-114.

DRIFT, J. VAN DER, 1951. — Analysis of the animal community in a beech forest floor. *Tijdschr. Ent.*, **94** : 1-168.

DUNGER, W. & ENGELMANN, H. D., 1978. — Testversuche mit immissiongeschützen Bodenfallen für Mikroarthropoden. *Pedobiologia*, **18** : 448-454.

DUNGER, W. & STEINMETZGER, K., 1981. — Ökologische Untersuchungen an Diplopoda einer Rasen-Wald-Catena im Thüringer Kalkgebiet. *Zool. Jahrb. Abt. Syst. Ökol. Geogr. Tiere*, **108** : 519-533.

Source : MNHN, Paris

FAIRHURST, C. P., 1979. — The distribution of Millipedes on a Lincolnshire sand dune system. *In* : M. CAMATINI, *Myriapod Biology*. London, Academic Press : 241-250.

FICHTER, E., 1941. — Apparatus for the comparison of soil surface arthropod populations. *Ecology*, **22** : 338-339.

FRANKE, U. & FRIEBE., B., 1983. — Erfassung der Makrofauna eines Buchenwaldbodens mittels Handauslese und Barbenfallen. *Verh. Dtsch. Zool. Ges.*, **1983** : 216.

FRANKE, U., FRIEBE B. & BECK, L., 1988. — Methodisches zur Ermittlung der Siedlungsdichte von Bodentieren aus Quadratproben und Barbenfallen. *Pedobiologia*, **32** : 253-264.

FRIEBE, B., 1983. — Zur Biologie eines Buchenwaldbodens 3. *Die Käferfauna. Carolinea* , **41** : 45-80.

GARAY, I., 1980. — Etude d'un écosystème forestier mixte. II. - Les sols. *Rev. Ecol. Biol. Sol*, **17** : 525-541.

GARAY, I., MOLLON A. & FLOGAITIS, E., 1986. — Etude d'une litière forestière mixte à charme (*Carpinus betulus* L.) et chêne (*Quercus sessiliflora* Smith). II. - Succession des macroarthropodes au cours de la décomposition. *Acta Œcologica, Œcol. Gener.*, **7** : 263-288.

GARAY, I., NAZOA S. & ABBADIE, L., 1986. — Etude d'une litière forestière mixte à charme et à chêne. I. - Décomposition de la matière organique et dynamique des éléments biogènes. *Acta Œcologica, Œcol. Gener.*, **7** : 151-169.

GEOFFROY, J. J., 1981a. — Etude d'un écosystème forestier mixte. V. Traits généraux du peuplement de diplopodes édaphiques. *Rev. Ecol. Biol. Sol*, **18** : 357-372.

GEOFFROY, J. J., 1981b. — Modalités de la coexistence de deux diplopodes, *Cylindroiulus punctatus* (Leach) et *Cylindroiulus nitidus* (Verhoeff), dans un écosystème forestier du Bassin Parisien. *Acta Œcologica, Œcol. Gener.*, **2** : 227-243.

GEOFFROY, J. J., 1985. — Les diplopodes d'un écosystème forestier tempéré : répartition spatio-temporelle des populations. *Bijdragen tot de Dierkunde*, **55** : 78-87.

GEOFFROY, J. J., CÉLÉRIER, M. L., GARAY, I., RHERISSI S. & BLANDIN, P., 1987. — Approche quantitative des fonctions de transformation de la matière organique par des macroarthropodes saprophages (Isopoda et Diplopoda) dans un sol forestier à moder : protocoles expérimentaux et premiers résultats. *Rev. Ecol. Biol. Sol*, **24** : 573-590.

GEOFFROY, J. J., CHRISTOPHE, T., MOLFETAS S. & BLANDIN, P., 1981. — Etude d'un écosystème forestier mixte. III. Traits généraux du peuplement de Macroarthropodes édaphiques. *Rev. Ecol. Biol. Sol*, **18** : 39-58.

GILBERT, O., 1956. — The natural histories of four species of *Calathus* (Col. Carabidae) living on sand dunes in Anglesey, North Wales. *Oikos*, **7** : 22-47.

GILLON, Y. & GILLON, D., 1976. — Comparaison par piégeage des populations de Diplopodes Iuliformes en zone de végétation naturelle et champ d'arachide. *Cahiers ORSTOM, sér. Biol.*, **XI** : 121-127.

GIST, C. S. & CROSSLEY, D. A., 1973. — A method for quantifying pitfall trapping. *Environ. Entomol.*, **2** : 951-952.

GREENSLADE, P. & GREENSLADE, P. J. M., 1971. — The use of baits and preservatives in pitfall traps. *J. Aust. Ent. Soc.*, **10** : 253-260.

GREENSLADE, P. J. M., 1964. — Pitfall trapping as a method for studying populations of Carabidae. *J. Anim. Ecol.*, **33** : 301-310.

HAACKER, U., 1968. — Descriptive, experimentelle und vergleichende Untersuchungen zur Autökologie Rhein-mainischer Diplopoden. *Oecologia* , **1** : 87-129.

HEATH, J., BOCOCK K. L. & MOUNTFORD, M. D., 1974. — The life-history of the millipede *Glomeris marginata* (Villers) in North-West England. *Symp. Zool. Soc. London* , **32** : 433-462.

HUSSON, R., 1937. — Reproduction non saisonnière des polydesmidés (Dipl.) des galeries de mines. *Bull. Soc. Sci. Nancy*, **7** : 195-198.

JANATI-IDRISSI, A., 1988. — Analyse du rôle des diplopodes en région méditerranéenne et influence de l'impact humain sur leurs communautés. Thèse de Doctorat, Ecologie, Montpellier III, 229 pp.

JOOSE, E. N. G. & KAPTEIJN, J. M., 1968. — Activity-Stimulating phenomena caused by field-disturbance in the use of pitfall-traps. *Oecologia*, **1** : 385-392.

KACZMAREK, W., 1978. — Die lokomotorische Aktivität der Bodenfauna als Parameter der trophischen Struktur und der Sukzession von Waldökosystem. *Pedobiologia*, **18** : 434-441.

KORSOS, Z., 1991. — Abundance and seasonal activity of millipedes in a dolomitic grassland community (Diplopoda). *Annls. hist.-nat. Mus. natn. Hung.*, **83** : 239-244.

KURNIK, I., 1985. — Über Diplopoden aus Barberfallen im Bereich der Grossglockener - Hochalpenstrasse (Kärnten, Österreich). *Carinthia II*, **175** : 271-283.

KURNIK, I., 1988. — Über Diplopoden von Xerotherm und Kulturstandarten bei Albiens (Südtirol). *Ber. nat.-med. Verein Innsbruck*, **75** : 109-113.

KURNIK, I. & THALER, K., 1985. — Weitere Diplopoden-Fallenfänge in Nordtirol (Österreich) (Myriapoda : Diplopoda). *Ber. nat.-med. Verein Innsbruck*, **72** : 145-154.

Source : MNHN, Paris

LE BERRE, J. R., 1969. — Les méthodes de piégeage des invertébrés. *In* : LAMOTTE, M. & BOURLIERE, F., *Problèmes d'écologie : l'échantillonnage des peuplements animaux des milieux terrestres.* Paris, Masson : 55-96.

LECORDIER, C. & BENEST., G., 1982. — Etude d'un écosystème forestier mixte. VI. Les carabiques (Col.). *Rev. Ecol. Biol. Sol*, **19** : 89-104.

LOKSA, I., 1988. — Über einige Athropoden-Gruppen aus dem Biosphäre-Reservat des Pilis-Gebirges (Ungarn). 1. Die Diplopoden, Chilopoden, Weberknechte und Spinnen vom Szamar-Berg und aus der Umgebung der Löss-Wand von Basaharc. *Opusc. Zool. Budapest*, **XXIII** : 159-176.

LUFF, M. L., 1968. — Some effects of formalin on the numbers of Coleoptera caught in pitfall traps. *Entomol. mon. Mag.*, **104** : 115-116.

LUFF, M. L., 1975. — Some features influencing the efficiency of pitfall traps. *Oecologia*, **19** : 345-357.

MADER, H. J. & MÜHLENBERG, M., 1981. — Artenzusammensetzung und Ressourcenangebot einer kleinflächigen Habitatinsel, untersucht am Beispiel der Carabidenfauna. *Pedobiologia*, **21** : 46-59.

MEYER, E., 1979. — Life cycles and ecology of high alpine Nematophora. *In* : M. CAMATINI, *Myriapod Biology*. London, Academic Press : 295-306.

MEYER, E., 1980. — Ökologische Untersuchungen an Wirbellosen des zentralalpinen Hochgebirges (Obergurgl, Tirol) : IV. Aktivitätsdichte, Abundanz und Biomasse der Makrofauna. *Veröffentl. Univ. Innsbruck,* **125** : 1-54.

MEYER, E., 1985. — Distribution, activity, life-history and standing crop of Julidae (Diplopoda, Myriapoda) in the central High Alps (Tyrol, Austria). *Holarct. Ecol.*, **8** : 141-150.

MITCHELL, B., 1963. — Ecology of two carabid beetles, *Bembidion lampros* and *Trechus quadristriatus. J. Anim. Ecol.*, **32** : 377-392.

MOLFETAS, S., 1982. — Etude d'un écosystème forestier mixte. VIII. - Les Isopodes. *Rev. Ecol. Biol. Sol*, **19** : 427-438.

MOLLON, A., 1982. — Etude d'un écosystème forestier mixte. VII. - Composition et phénologie du peuplement des Diptères à larves édaphiques. *Rev. Ecol. Biol. Sol*, **19** : 289-306.

MOLLON, A., 1983. — Etude d'un écosystème forestier mixte. IX. - Les Diptères édaphiques, structure temporelle du peuplement larvaire. *Rev. Ecol. Biol. Sol*, **20** : 367-383.

MURDOCH, W. W., 1966. — Aspects of the population dynamics of some marsh Carabidae. *J. Anim. Ecol.*, **35** : 127-156.

PANTIS, J. D., STAMOU G. P. & SGARDELIS., S. S., 1988. — Activity patterns of surface ground fauna in Asphodel deserts (Thessalia, Greece). *Pedobiologia*, **32** : 81-87.

PARK, O., 1935. — Studies on nocturnal ecology. III. Recording apparatus and further analysis of activity rhythm. *Ecology*, **16** : 152-163.

PARK, O., LOCKETT J. A. & MYERS., D. J., 1931. — Studies on nocturnal ecology with special reference to climax forest. *Ecology*, **12** : 709-727.

PEDROLI-CHRISTEN, A., 1978. — Contribution à la connaissance du développement post-embryonnaire de *Craspedosoma alemannicum* Verhoeff et de *Xylophageuma zschokkei* Bigler (Diplopoda, Nematophora) dans une tourbière du Haut-Jura. *Rev. Suisse Zool.*, **85** : 673-679.

PEDROLI-CHRISTEN, A., 1981. — Étude des peuplements de diplopodes dans six associations forestières du Jura et du Plateau Suisse (Région Neuchâteloise). *Bull. Soc. Neuchâteloise Sci. nat.*, **104** : 89-106.

PEDROLI-CHRISTEN, A. & A. SCHOLL., 1990. — Ecological and genetic studies on parapatric *Rhymogona silvatica* Roth. and *R. cervina* Verh. (Diplopoda : Craspedosomatidae) with special reference to hybrid populations in a zone of contact. *Rev. Suisse Zool.*, **97** : 349-359.

PEITSALMI, M., 1981. — Population structure and seasonal changes in activity of *Proteroiulus fuscus* (Am Stein) (Diplopoda, Blaniulidae). *Acta Zool. Fenn.*, **161** : 1-66.

RUSDEA, E., 1992. — Stabilisierende Selektion bei Microphthalmen Höhlentieren : Untersuchungen zur Tages-Zeitlichen Aktivitätsverteilung und Populationsdynamik von *Lemostenus schreibersi* (Küster) (Carabidae). *Mém. Biospéol.*, **19** : 1-110.

SAHLI, F., 1969. — Sur la biologie sexuelle (accouplement, ponte, instincts sexuels) du Diplopode *Polydesmus angustus* Latzel. *Rev. Ecol. Biol. Sol*, **6** : 437-445.

SNIDER, R., 1981. — The reproductive biology of *Polydesmus inconstans* (Diplopoda: Polydesmidae) at constant temperatures. *Pedobiologia*, **22** : 354-365.

SOUTHWOOD, T. R. E., 1978. — *Ecological Methods, with particular reference to the study of Insect populations (2nd ed.).* London, Methuen & C°.

SPELDA, J., 1993. — Hundert- und Tausendfüsser aus Missen der Umgebung von Oberreichenbach, Lkr. Calw (Chilopoda, Diplopoda). *Beih. Veröff. Naturschutz Landschaftspfelge Bad.-Württ.*, **73** : 399-402.

Source : MNHN, Paris

STEINER, P., WENZELAND, F. & BAUMERT., D., 1963. — Zur Beeinflussung der Arthropodenfauna nordwest deutscher Kartoffelfelder durch die Andwendung synthetischer Kontaktinsektizide. *Mitt. biol. BundAnst. Ld.-u. Forstw., Berlin*, **109** : 1-38.

SZEKELYHIDY, E. H. & LOKSA, I., 1979. — Oniscoiden-, Diplopoden- und Chilopoden- Gemeinschaften im Untersuchungsgebiet "Sikfökut-Projekt" (Ungarn). *Opusc. Zool. Budapest*, **XVI** : 151-174.

TOPPING, C. J. & SUNDERLAND, K. D., 1992. — Limitations to the use of pitfall traps in ecological studies examplified by a study of spiders in a field of winter wheat. *J. Appl. Ecology*, **29** : 485-491.

VAJDA, Z. & HORNUNG, E., 1991. — Temporal and spatial pattern of a diplopod population (*Megaphyllum unilineatum* (C.L. Koch) in a sandy grassland. *Acta Biol. Szeged.*, **37** : 75-81.

VERHOEFF, K. W., 1928. — Diplopoda 1. *In* : H. G. BRONN's *Klassen und Ordnungen des Tierreichs*, **5**, Leipzig, Akademische Verlagsgesellschaft : 1-1072.

WILLIAMS, G., 1958. — Mechanical time-sorting of pitfall captures. *J. Anim. Ecol.*, **27** : 27-35.

WILLIAMS, G., 1959. — The seasonal and diurnal activity of the fauna sampled by pitfall traps in different habitats. *J. Anim. Ecol.*, **28** : 1-13.

Source : MNHN, Paris

Traces de l'activité de diplopodes dans des sols et des sédiments karstiques du Maroc Atlantique

Colette JEANSON *, Hsaïn EL AISSAOUI ** Jean-Pierre ADOLPHE **

* CNRS, Laboratoire d'Écologie Générale, Muséum National d'Histoire Naturelle
4, avenue du Petit Château, F- 91800 Brunoy, France
** Laboratoire de Géomicrobiologie, Université Pierre & Marie Curie, 4, place Jussieu, F-75005 Paris, France

RÉSUMÉ

Une étude pluridisciplinaire et multiscalaire conduit les auteurs à utiliser des données de la pédozoologie pour interpréter des observations sédimentologiques et géologiques. Les concrétions carbonatées des sédiments karstiques, des agrégats terreux de sols actuels et les déjections obtenues expérimentalement par élevage de *Glomeris marginata* (Diplopoda, Glomerida), présentent une très nette analogie morphologique et physicochimique. Des relations sont établies entre les phénomènes de pédobioturbation, paléobioturbation et sédimentation.

ABSTRACT

Activity traces of millipedes in soils and karstic sediments in Atlantic Morocco.

The authors are carrying into effect a pluridisciplinary and multiscalar approach for using pedozoology data to interpret sedimentological and geological observations. Carbonated concretions of karstic sediments, earthy aggregates of Present soils, and experimental feacal pellets of *Glomeris marginata* (Diplopoda, Glomerida) show a very clear morphological and physico-chemical analogy. Relationships are then identified between pedobioturbation, paleobioturbation and sedimentation phenomena.

INTRODUCTION

Les formations carbonatées continentales du Haut-Atlas occidental marocain montrent un développement spatial important et présentent une grande diversité de faciès : des revêtements pelliculaires sur les galets des oueds, des croûtes en dalles compactes, des croûtes zonaires laminées, des croûtes conglomératiques, des édifices travertineux et des concrétionnements pédo-karstiques (ADOLPHE, 1981 ; HOURIMÈCHE, 1988). La démarche initiale de cette étude consiste à circonscrire et à décrire sur le terrain le domaine des concrétionnements pédo-karstiques constitués par des assemblages de concrétions carbonatées de quelques millimètres en forme de "cocons". Cela dans le but de tenter de comprendre leur origine, les conditions de leur mise en place et leurs relations avec les microorganismes de leur environnement (ADOLPHE *et al.*, 1995).

JEANSON, C., EL AÏSSAOUI, H. & ADOLPHE, J.-P., 1996. — Traces de l'activité de diplopodes dans des sols et des sédiments karstiques du Maroc atlantique. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 555-560. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

A cette occasion, nous avons également mis en évidence le rôle de myriapodes diplopodes dans l'élaboration de telles concrétions. Ce travail concerne des échantillons provenant de deux des sites de l'étude entreprise sur les concrétionnements carbonatés dans le Haut-Atlas.

MATÉRIEL ET MÉTHODES

Localisation des sites : Imouzzer et Taliwine

Le site d'Imouzzer fait partie du domaine des Ida-ou-Tanane, zone la plus montagneuse de l'Atlas atlantique, au cœur d'un anticlinal incisé par l'Oued Tidili qui entame les calcaires du Lias supérieur jusqu'au contact avec les argiles du Lias inférieur.

La coupe type du "gisement" à concrétions carbonatées est située sur la rive gauche de l'oued Tidili à 1 km de la cascade d'Imouzzer. Sur les collines, un paysage de glacis-cônes où les cavités (lapiès) de 1 à 5 cm de profondeur sont remplies d'un sol rouge résiduel à concrétions en "cocons" de couleur allant du rouge au noir. Au fond de la combe, l'oued entaille des terrasses quaternaires cultivées où les sols limoneux actuels contiennent aussi des concrétions en forme de "cocons". Cylindriques ou cylindroconiques, leur taille varie de 1 mm à 2 mm de longueur.

Le site de Taliwine sur le flanc sud du Haut-Atlas occidental présente un "gisement" moins important que le précédent. La coupe représentative est levée près de Bouyalgua à 1 km à l'ouest de Taliwine.

Au laboratoire. Analyse morphologique, minéralogique et géomicrobiologique.

Les échantillons entiers sont photographiés puis examinés à la loupe binoculaire. Des lames minces y sont taillées après induration puis examinées au microscope polarisant pour l'identification des matériaux organiques et des minéraux.

Le microscope électronique à balayage apporte un complément d'informations au niveau ultramicroscopique sur l'état de surface des concrétions et sur les microorganismes qui s'y développent.

RÉSULTATS

Sur le terrain

A Imouzzer, les concrétions sont localisées dans la partie marno-calcaire des coupes selon un système lenticulaire à répartition discontinue. La taille des lentilles varie de 1 cm d'épaisseur et 10 cm de longueur à 40 cm d'épaisseur et 150 cm de longueur. Ces dernières sont situées au sommet des coupes et parfois superposées par groupe de deux ou trois. Les concrétions y sont regroupées en amas irrégulièrement consolidés par une matrice également marnocalcaire.

La majorité des lentilles de concrétions est de couleur blanche et grise ; les autres sont colorées de jaune à rouge-brun par des oxydes de fer. Souvent, la base des lentilles est tapissée d'une croûte pelliculaire de quelques millimètres (croûte zonaire).

A la partie sommitale des mêmes coupes, un banc de calcaire dur de 30 cm environ est surmonté d'un sol résiduel de couleur rouge qui remplit des cavités de dissolution (lapiès). Ce paléosol renferme aussi des concrétions cylindriques, cylindroconiques, voire ovoïdes de couleur rouge à noire.

A Taliwine, les lentilles de concrétions sont localisées au sommet de la coupe dans une formation marno-schisteuse. Elles ont de 1 à 10 cm d'épaisseur et de 20 à 150 cm de longueur et sont disposées de façon discontinue sans aucun regroupement particulier. Les concrétions ont la même forme que les précédentes et sont de couleur grise et blanche.

Au laboratoire

A la loupe binoculaire, on note une homogénéité morphologique des concrétions et une variabilité de leur couleur et de leur taille. La forme est cylindroconique, ovoïde ou subsphérique ; une extrémité est arrondie avec une légère dépression centrale, l'autre présente souvent une petite protubérance subtriangulaire légèrement incurvée (Fig. 1). Leur taille varie de 1 mm x 0,5 mm à 2 mm x 1 mm. Dans l'ensemble, celles d'Imouzzer sont plus grandes que celles de Taliwine.

La couleur des concrétions varie avec le milieu où elles se trouvent. Ainsi, dans les sols rouges remplissant les cavités de dissolution (lapiès), elles sont rouges ou noires. Dans les sols cultivés des terrasses, elles sont grises ou noires. Dans les lentilles enclavées dans les formations

Source : MNHN, Paris

carbonatées, elles sont en général blanches mais il existe aussi quelques lentilles beige-rosé ou rouges colorées par les oxydes de fer.

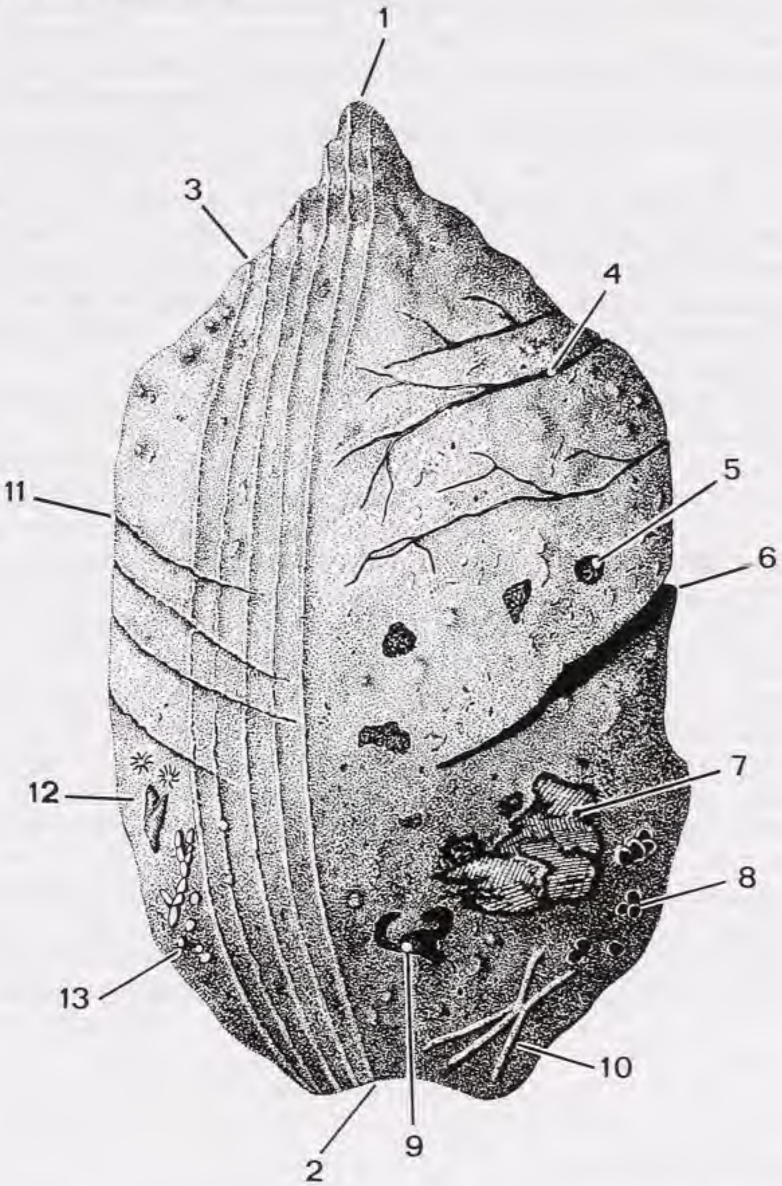


FIG. 1. — Concrétion - déjection cylindroconique de *Glomeris* sp. (Myriapode, Diplopode) ; longueur 1 à 2 mm ; schéma de synthèse de la surface d'après photos à la loupe binoculaire et au microcope à balayage (m.e.b.) : 1. extrémité antérieure à protubérance conique. 2. extrémité postérieure à dépression centrale. 3. rainures et cannelures entre les deux extrémités. 4. traces de mycélium. 5. taches de carbonate de calcium ou d'oxydes ferriques. 6. cassure. 7. débris végétaux. 8. turricules de nématodes, à la surface. 9. id. dans une cavité. 10. canalicules, sillons, pistes de nématodes. 11. stries obliques de frottement. 12. cristaux de calcite, en rosette, en baguette, au m.e.b. 13. bactéries filamenteuses et en sphérules, au m.e.b.

FIG. 1. — Cylindroconic fæcal pellet of Glomeris *sp. (Diplopoda); length: 1 to 2 mm. Synthetic drawing after photographs (Stereomicroscope and SEM). 1. anterior end with cone-shaped protuberance. 2. posterior end with central depression. 3. grooves and striations between the two ends. 4. mycelium traces. 5. stains of calcium carbonate or ferric oxydes. 6. break. 7. vegetal fragments. 8. nematod excreta, on the surface. 9. id., in a cavity. 10. small grooves and nematod trails. 11. rubbing oblique scores. 12. rosette and stick-shaped calcite crystal, SEM. 13. filamentous and spheruleous bacteria, SEM.*

Source : MNHN, Paris

La surface des concrétions est ornementée de traces, d'empreintes, de cavités, de minuscules monticules, de fins débris végétaux. Des réseaux de fins sillons et des canalicules ramifiés, parfois colorés en blanc ou en noir, s'insinuent entre des corpuscules sphériques isolés ou regroupés par trois ou quatre. Les réseaux sont discontinus et ne couvrent qu'une partie de la surface de la concrétion. Une minuscule cavité est parfois présente, proche de l'extrémité arrondie de la concrétion et de très petits turricules en garnissent souvent le fond (Fig. 1 [9]).

La microtopographie de la surface des concrétions est aussi marquée par des cannelures et des rainures plus ou moins rectilignes qui rejoignent les deux extrémités à intervalle régulier (Fig. 1[3]). Les débris végétaux ou leurs empreintes, des fragments translucides de filaments mycéliens sont nettement visibles. Il existe aussi des microcassures, fractures, fissures parfois remplies d'une substance noire (Fig. 1[6]) et de fines cristallisations en baguette et en rosette.

Autant de traces des étapes successives de la construction et de la mise en place de la concrétion, de l'impact de l'environnement et de l'évolution consécutive qu'il va falloir interpréter dans le temps et l'espace.

Au microscope polarisant, l'examen des lames minces fait apparaître trois sortes de concrétions : minérales, organiques, organominérales.

Les concrétions minérales sont blanches, constituées de micrite, de microsparite, de rares cristaux de quartz, de quelques constituants noirs amorphes de matière organique décomposée. La matrice est une calcite et l'ensemble de la lame présente une structure compacte et homogène.

Les concrétions brun-noir contiennent des débris organiques allongés, souvent disloqués, de couleur noire, jaune ou brun-rouge où les tissus végétaux sont encore visibles. Quelques cristaux de quartz et de micrite y sont parfois associés. Ces concrétions sont poreuses et l'ensemble de la lame présente une structure alvéolaire peu indurée.

Les concrétions grises ont une composition mixte organo-minérale. La micrite et la microsparite sont associées à une matière organique amorphe et sans structure visible ou à des fantômes de débris organiques. Ces concrétions ont une structure relativement compacte.

Les concrétions brun-rouge appartiennent à l'une des catégories ci-dessus. Elles ont une matrice colorée par les oxydes de fer et sont beaucoup plus dures que les précédentes et résistent mieux à la pression

Au microscope électronique à balayage, la surface des concrétions présente: 1) des corpuscules sphériques de 0,1 µm à 1 µm en chapelet, 2) des enchevêtrements de filaments mycéliens, 3) des réseaux de sillons superficiels striés perpendiculairement à leur axe. Ces divers microorganismes et ces microtraces sont fortement minéralisés et associés à des aiguilles de calcite.

INTERPRÉTATION

Les concrétions-agrégats-déjections

Les concrétions de ces sols et sédiments sont comparables par leur taille, leur forme et quelques traits de leur micromorphologie externe, aux agrégats terreux décrits dans des sols bruns forestiers (JEANSON, 1981). Des agrégats identiques sont aussi construits par des myriapodes diplopodes, *Glomeris marginata* élevés dans des microcosmes en conditions contrôlées selon la méthode de pédozoologie expérimentale (JEANSON, 1968).

D'autres types d'agrégats, construits par vingt cinq espèces d'invertébrés terricoles et vasicoles actuels, ont été sélectionnés. Ces modèles sont proposés pour, éventuellement, servir à l'interprétation des phénomènes de biostructuration et bioturbation dans les paléosols étudiés en Géologie de la Préhistoire (JEANSON, 1987).

Dans les sols actuels, des agrégats analogues sont élaborés et construits par des *Glomeris* et sont en réalité des déjections déposées dans les premiers centimètres. Le matériel consommé y est encore bien visible : de nombreux fragments végétaux sont reconnaissables à leur structure

Source : MNHN, Paris

cellulaire et souvent associés à une matière minérale limono-argileuse. Ces agrégats-déjections sont ainsi des indices : par leur forme, des animaux terricoles qui les ont construits ; par leur constituants, du milieu d'où ils proviennent ; par l'état de leur surface, de l'évolution de leur environnement.

La couleur et l'état de la surface des concrétions peuvent ainsi être interprétées à la lumière des données biopédologiques actuelles :

- les concrétions blanches sont formées surtout de carbonate de calcium, les noires, de matière organique humifiée, les grises, d'un mélange des deux ;
- les concrétions rouges, brunes, beiges sont colorées par des oxydes de fer à des degrés de concentration variables. Cette diversité de couleurs est à mettre en relation avec l'importance du déplacement des oxydes de fer et leur accumulation dans les concrétions.

Dans l'état actuel de nos investigations, la chronologie de la coloration serait la suivante : des concrétions-déjections élaborées à partir du sédiment du sol sont de la couleur brunâtre de ce dernier, par la suite elles blanchissent progressivement en se minéralisant par le carbonate de calcium sous l'influence des bactéries calcifiantes. Les concrétions imprégnées d'oxydes de fer prennent une coloration brun-rouge, parfois marquée de taches blanches, indices d'une carbonatation en cours.

L'interprétation des microtraces de la surface des concrétions est biologique ou physicochimique.

Des cannelures joignent les deux extrémités ; elles sont plus marquées sur la partie conique des concrétions et dues à l'empreinte de la partie terminale du tube digestif des *Glomeris.* La partie conique émise en dernier correspond ainsi à la partie antérieure de l'animal. Cette extrémité est parfois érodée ou absente ce qui donne à la concrétion une forme subovoïde, et pourrait constituer un indice de déplacement par ruissellement.

Les sillons marqués en creux et peu ramifiés pourraient être des traces laissées par des nématodes. Une trentaine d'espèces de ces vers bactériophages et mycophages peuvent proliférer dans les déjections actuelles de *Glomeris hexasticha* (TAJOVSKY *et al.*, 1992). Ils pourraient aussi être à l'origine des petits turricules et de la logette située à l'extrémité arrondie.

Les sillons peu marqués et plus ramifiés pourraient être des traces laissées par des filaments mycéliens. En effet, dans des déjections actuelles de *Glomeris marginata*, une quinzaine d'espèces de champignons se succèdent au cours de leur décomposition (NICHOLSON *et al.*, 1966). Les petits lambeaux transparents et luisants qui subsistent par endroits sur les concrétions-déjections pourraient être des vestiges des réseaux mycéliens. Ils sont parfois colorés en noir par la matière organique issue de leur décomposition ou de substances organiques qui ont migré. Ils peuvent être aussi colorés en blanc par le carbonate de calcium très visible sur les concrétions ferruginisées. Les corpuscules sphériques en chapelet sont des bactéries ou des cyanobactéries. Cette microflore est souvent associée à une forte minéralisation caractéristique des dépôts microkarstiques et pédologiques. Les cristaux calciques en baguettes ou en rosettes, à la surface des concrétions-déjections, sont d'origine bactérienne (ADOLPHE *et al.*, 1989).

Les lentilles et amas de concrétions

Les concrétions carbonatées s'accumulent en amas en forme de lentilles, dans des fentes ou des cavités du réseau karstique souvent délimitées par de fins dépôts calcaires en lamelles rubanées.

L'hypothèse proposée pour interpréter la genèse de ces formations géologiques externes fait appel à des phénomènes pédologiques, biologiques et climatiques : un couvert végétal forestier et une litière abondante ont pu favoriser le développement des populations de diplopodes. Des phases de destruction de la forêt ont pu favoriser l'érosion des sols et le

Source : MNHN, Paris

ruissellement, l'entraînement et l'accumulation des déjections de diplopodes dans des zones préférentielles du réseau karstique.

Les déjections riches en matière organique déja décomposée et associée au mucus digestif des diplopodes constituent des micro-milieux propices au développement des microorganismes. La circulation de solutions bicarbonatées et ferreuses induit ensuite une carbonatogenèse bactérienne et une concentration d'oxydes ferriques. Les déjections, d'abord organiques, deviennent organominérales puis se transforment en concrétions minérales, carbonatées et/ou ferriques.

CONCLUSION

Les traces de l'activité des diplopodes dans des sols actuels et des sols expérimentaux sont matérialisées par des biostructures caractéristiques ; des agrégats terreux construits par ces arthropodes sont en réalité des déjections. Celles des *Glomeris* actuels sont comparables aux concrétions carbonatées rassemblées dans des formations lenticulaires de sédiments karstiques du Haut-Atlas Atlantique.

La nature, la forme, la structure, le degré d'altération et l'agencement spatial des matériaux minéraux et organiques de ces concrétions-agrégats-déjections permettent de proposer une chronologie des phénomènes qui sont à l'origine de leur apparition dans l'environnement.

Un champ d'investigation interdisciplinaire entre les Sciences de la Terre et les Sciences de la Vie, la “Pédozoologie”, a ainsi fourni des bases pour l'interprétation de faits sédimentologiques et géologiques. Cette démarche pourrait être appliquée à d'autres formations sédimentaires et se baser sur d'autres analogies avec des biostructures construites par divers animaux terricoles.

REMERCIEMENTS

Nous remercions vivement Jacques REBIÈRE, dessinateur au M.N.H.N., Laboratoire de Zoologie-Arthropodes (Paris), pour sa réalisation du schéma de synthèse.

RÉFÉRENCES

ADOLPHE, J. P., 1981. — Observations et expérimentations géomicrobiologiques et physico-chimiques des concrétionnements carbonatés continentauxs actuels et fossiles. Thèse Sciences, UPMC, *Mém. Sci. Terre*, Paris VI, 339 pp.

ADOLPHE, J. P., HOURIMECHE, A., LOUBIERE, J. F., PARADAS, J. & SOLEILHAVOUP, F., 1989. — Les formations carbonatées continentales d'Afrique du Nord. *Bull. Soc. géol. Fr.*, (8), **V** : 55-62.

ADOLPHE, J. P., EL AISSAOUI, H., HOURIMECHE, A., PARADAS, J., SOLEILHAVOUP, F. & JEANSON, C., 1995. — Contribution à l'étude des biostructures. Exemple marocain. *In* : *Bassins sédimentaires africains. Actes du 4ème Colloque de Géologie africaine.* [118ème congrès national des sociétés historiques et scientifiques. Pau, 25-29 octobre 1993], Paris, Éditions du CTHS : 259-268.

HOURIMECHE, A., 1988. — *Étude sédimentologique et géomicrobiologique des dépôts quaternaires de la région d'Essaouira (Maroc).* Thèse Sciences, UPMC, Paris VI, 222 pp.

JEANSON, C., 1968. — Essai de Pédozoologie expérimentale. Morphologie d'un sol artificiel structuré par les Lombricidés. *Mém. Mus. natn. Hist. nat., A,* **46** : 211-357.

JEANSON, C., 1981. — Structuration du sol par la faune terricole. Incidences sur les concentrations organominérales. *In* : *Migrations organominérales dans les sols tempérés. Colloque de Nancy 1979.* Nancy, Editions du CNRS : 114-123.

JEANSON, C., 1987. — Biostructures construites par la faune dans des sols et des sédiments actuels. Leur utilisation en Préhistoire. *In* : *Géologie de la Préhistoire*, Paris, Géopré : 725-735.

NICHOLSON, P. B., BOCOCK, K. L. & HEAL, O. W., 1966. — Studies on the decomposition of the faecal pellets of a millipede (*Glomeris marginata* (Villers)). *J. Ecol.*, **54** : 755-766.

TAJOVSKY, K., SANTRUCKOVA, H., HANEL, L., BALIK, V. & LUKESOVA, A., 1992. — Decomposition of faecal pellets of the millipede *Glomeris hexasticha* (Dipopoda) in forest soils. *Pedobiologia* , **36** : 146-158.

Source : MNHN, Paris

Feeding Rates and Nutrient Assimilation in the Millipede *Jonespeltis splendidus* (Diplopoda, Paradoxosomatidae)

Kubra BANO

Department of Zoology, University of Agricultural Sciences, G.K.V.K., Bangalore, 560065 India

ABSTRACT

Laboratory studies have been conducted on the feeding and egestion of the millipede *Jonespeltis splendidus*. The millipedes were found highly specific in their diet. Ingestion and egestion rates varied with the component of the diet as well as with the sex of the individuals. Acceptability of the food depended on the moisture content and the material softness. Palatability was based on the nitrogen levels of the food. Egestion rates were directly proportional to the quantity ingested. Further, the percentage of assimilation was found to be higher with litter. The nutrient uptake by the millipede was recorded at the rate of 62, 26 and 12% with respect to proteins, fats and carbohydrates. With the feeding recorded rates the consumption by the millipede was estimated to be about 4-5 grams of dry litter per year per millipede. As the sampled population density ranged near 200 millipedes per square metre, the rate of the litter breakdown would approach 1 kg per year, per suare metre.

RÉSUMÉ

Taux d'ingestion et d'assimilation chez le diplopode *Jonespeltis splendidus* (Diplopoda, Paradoxosomatidae).

Des études en laboratoire ont été menées sur la consommation et la réjection chez le diplopode *Jonespeltis splendidus* qui montre une relation hautement spécifique vis-à-vis de son régime alimentaire. Les taux d'ingestion et d'égestion varient avec la composition de la nourriture et avec le sexe des individus. L'appétance pour la nourriture dépend du taux d'humidité et de la souplesse du matériel, de même que de son contenu en azote. Le taux de consommation correspond à la quantité de matériel ingéré ; toutefois, le pourcentage d'assimilation paraît plus élevé dans le cas de consommation de litière. On a enregistré pour le diplopode un apport nutritif de 62, 26 et 12% en rapport avec les protéines, les lipides et les glucides. En fonction des taux d'ingestion mesurés, la consommation par le diplopode est estimée à environ 4-5 grammes de litière sèche par an et par individu. La densité de la population étant estimée à environ 200 diplopodes par mètre carré, la dégradation annuelle de la litière s'établit autour de 1 kg par mètre carré.

INTRODUCTION

Jonespeltis splendidus (Verhoeff), a soil and litter dwelling millipede, is normally found in large populations under dead and decaying organic matter, under humus layers on the forest floors, in small number underneath pots in the gardens, and under stones and logs where moisture is conserved. It is also found to occur in cow dung pits. Large populations are always associated with availability of organic matter and high moisture levels. Dry litter drives the

BANO, K., 1996. — Feeding rates and nutrient assimilation in the millipede *Jonespeltis splendidus* (Diplopoda, Paradoxosomatidae). *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 561-564. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

population away. It feeds on the substratum on which it lives and deposits pad like faecal matter on the surface that can be easily picked up as crust.

Reports are available on the food consumption and assimilation in other millipedes (see, among others, BLOWER, 1974; KAYED, 1978; BRUGGL, 1992). As *J. splendidus* is known to be a regulator and decomposer in its habitat, it was decided to record its feeding rates and nutritive requirements which were correlated to assess the fertility levels of its surroundings.

MATERIAL AND METHODS

The millipedes were collected from gardens and fields in and around Bangalore and were held in vivaria on moist garden soil (alfisol), with a layer of moist decomposing organic litter.

Before the beginning of the present experiment, the millipedes were fed on wet filter paper to clean their guts. Determination of feeding and defecation rates: one kg of finely sieved soil was spread uniformly in a glass trough 305 mm in diameter and 150 mm deep. The soils were moistened to 50% level.

100 adult millipedes, which were fed on wet filter paper earlier, were allowed to feed on the soils for four hours. After four hours of feeding the millipedes were picked and transferred to clean Petri dishes (150 mm diameter) for two hours. The covered Petri dishes were lined with wet filter papers for maintaining the humidity. The faecal pellets that were deposited in the Petri dishes were collected. The feeding and egestion rates were determined gravimetrically.

Similar experiments were conducted with Mango leaf litter. 1 kg of fine sand was uniformly laid in each glass trough and moistened to 50% level. About 200 g of wet decomposing mango leaf litter was deposited over the sand bed. The experiment then went on as mentioned earlier.

The determination of feeding rates was carried with known quantities of moistened soil and decomposing litter alone (separately) with known number of millipedes in small plastic boxes. Every day the material was weighed after picking the millipedes and separating the faeces. The difference in weight between the feed material before and after feeding was recorded as the consumption. The moisture level was maintained by covering the containers with lids lined with wet polystyrene foam.

The containers used for the experiment were maintained at 25 ± 2°C. The experiments were conducted on round the clock basis. In darkness red light was used to record observations.

Protein, carbohydrates and fats were analysed bio-chemically by adopting standard techniques.

RESULTS

The recorded food intake and defecation of adult millipedes in relation to sex (Fig. 1), when soil was used as the medium, are given in Table 1. The rate of consumption of the males was higher than that of the females. The intake of soil was higher than that of the decomposing litter in both sexes. The millipedes feed on the soft tissue of the litter, avoiding the veins and the midrib, which are woody in nature. The intake of food was dependent on the nutritive value and also on the microbial fauna of the medium, which was also reported by BLOWER (1974).

TABLE 1. — Feeding and excretory rates (mg/day) of *Jonespeltis splendidus* (Mean result for 100 individuals).

Sex	Males		Females	
Feed	Soil	Mango litter	Soil	Mango litter
Ingestion	31.84	13.2	51.54	12.2
Egestion	24.83	3.3	31.95	4.5
% Assimilation	22	75	38	63

The active period of feeding was found to be the morning hours. The feeding rates recorded during these hours are given in Table 2.

Table 3 presents the proximate composition of the mango leaf litter and the excrements of the male and female millipedes. The composition of the excrements did not differ with reference to sex. The excrements contained more nitrogen than carbohydrates. The fat contents were significantly higher in the male excrements. This suggests that the female assimilated more fats than the males, perhaps as their energy requirements are more important during ovulation.

Source : MNHN, Paris

TABLE 2. — Feeding and excretory rates of *Jonespeltis splendidus* with soils in mg. per hour (forenoon) (Mean result for 100 individuals).

Hour	1	2	3	4	5	6
Consumption	9.6	6.6	11.33	6.6	5.3	8.2
Excretion	2.3	1.0	2.5	1.0	1.9	0.9

TABLE 3. — Composition of the mango leaf litter and faecal pellets of the millipede *Jonespeltis splendidus*.

Material	mg / 100 mg dry mass (X ± S.D. ; n=4)		
	Nitrogen	Soluble Carbohydrates	Total fats
Dry mango leaf	4.34	4.50	7.54
Faeces (Female)	2.95 ± 0.47	1.83 ± 0.38	2.72
Faeces (Male)	2.41 ± 0.81	1.77 ± 0.39	3.32

Table 4 demonstrates the daily caloric intake of adults. More ingestion was noted in both sexes for proteins than for fats and carbohydrates.

TABLE 4. — Caloric intake of *Jonespeltis splendidus* (Estimated).

Food	1st day		3rd day	
	Male	Female	Male	Female
Soluble Carbohydrates	4.7871	4.7709	1.0701	1.0683
Protein	31.9737	30.9207	8.3626	7.6960
Total fats	13.3851	13.6359	3.2368	3.2733

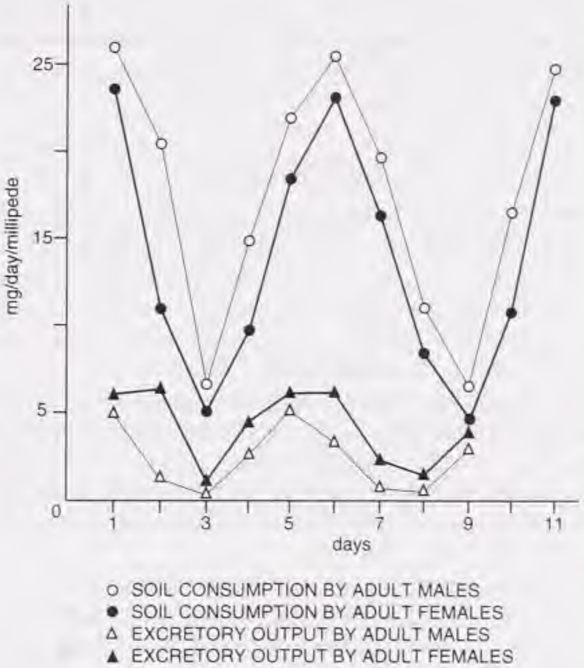


Fig. 1. — Soil ingestion and soil egestion by adult males and females of *Jonespeltis splendidus*, in relation to sex.

Source : MNHN, Paris

DISCUSSION

Earlier investigations have revealed that the millipede *Jonespeltis splendidus* is a saprophagous macroarthropod feeding selectively on decaying plant organic matter, and preferring Mango leaf litter, when choice is offered (BANO & KRISHNAMOORTHY, 1981). The feeding activity depends on the nitrogen content of the food source, which was evident when different types of litter, cow dung and soils were offered. In the present experiment, smaller intakes were recorded with litter, and larger intakes were associated with soils in which organic nitrogen and carbon contents were low. If the surface layer was covered with organic matter, the activity of the millipedes was restricted to the surface. When soils alone were offered the millipedes exhibited burrowing activity, which is indicative of foraging behaviour for organic matter. The consumption of soil was important in the absence of leaf litter. These features allow the millipedes to get their nutritive requirements. There was no significant difference in the litter intake between the sexes. The mango litter consumption was more or less equivalent in both the sexes, but the soil consumption varied. The assimilation varied with soil and litter. The energy requirements of the millipedes were obtained mostly from proteins (62%), followed by fats (26%) and carbohydrates (1%).

The role of arthropods and particularly diplopods in soil-litter system has been described in various ways (cf. CRAWFORD, 1992). They are considered as accelerators, regulators and decomposers. While working on the millipede *J. splendidus* the author has elaborated similar interpretation for the role of this millipede (BANO & KRISHNAMOORTHY, 1976, 1977; BANO, 1992). The feeding activity involved destruction of litter as these millipedes feed on the soft tissues, leaving the veins and the fibrous portions to decay further. They contribute to the transformation of the organic constituents, improving the humic part of the soils. Their direct effect is the acceleration of the formation of humus, and the indirect effect is the incrementing of the microflora through their faecal pellets. With the present data it could be calculated that a millipede consumes 4 to 5 g of leaf litter (dry mass) in a period of six months, which could be taken as the active period of the millipede's life cycle. The distribution of the species varies in relation to the nature of the soils and organic matter. A maximum of 200 individuals/m^2 was reported earlier (BANO & KRISHNAMOORTHY, 1985). This distribution would destruct about 1 kg of dry leaf litter per year, thus suggesting their role as decomposers in their habitats. Similar results were obtained by BLOWER (1974) with *Ophyiulus pilosus* regarding the mass of leaf consumed per year.

REFERENCES

BANO, K., 1992. — The role of the millipede *Jonespeltis splendidus* (Verhoeff) in an ecosystem (Diplopoda, Polydesmida, Paradoxosomatidae). *Ber. nat.-med. Verein Innsbruck*, **Suppl. 10** : 319-327.

BANO, K., BAGYARAJ, D. J. & KRISHNAMOORTHY, R. V., 1976. — Feeding activity of the millipede *Jonespeltis splendidus* Verhoeff and soil humification. *Proc. Indian Acad. Sci. (Animal Sci.)*, **83B** : 1-11.

BANO, K. & KRISHNAMOORTHY, R. V., 1977. — Changes in the composition of soils due to defæcation by the millipede *Jonespeltis splendidus* (Verhoeff). *Mysore J. Agric. Sci.*, **11** : 561-566.

BANO, K. & KRISHNAMOORTHY, R. V., 1981. — Consummatory responses of the millipede *Jonespeltis splendidus* (Verhoeff) in relation to soil organic matter. *Proc. Indian Acad. Sci. (Animal Sci.)*, **90** : 631-640.

BANO, K. & KRISHNAMOORTHY, R. V., 1985. — Reproductive strategy and life history of *Jonespeltis splendidus* (Verhoeff) (Diplopoda: Polydesmida) with environmental synchronisation. *J. Soil Biol. Ecol.*, **5** : 48-57.

BLOWER, J. G., 1974. — Food consumption and growth in a laboratory population of *Ophyiulus pilosus* (Newport). *Symp. Zool. Soc. Lond.*, **32** : 527-551.

BRUGGLE, K., 1992. — Gut passage, respiratory rate and assimilation efficiency of three millipedes from a deciduous wood in the Alps (Julidae, Diplopoda). *Ber. nat.-med. Verein Innsbruck*, **Suppl. 10** : 319-326.

CRAWFORD, C. S., 1992. — Millepedes as model detritivors. *Ber. nat-med. Verein Innsbruck*, **Suppl. 10** : 277-288.

KAYED, A. N., 1978. — Consumption and assimilation of food by *Ophyiulus pilosus* (Newport). *Abh. Verh. Naturwiss Ver. Hamburg*, **21/22** : 115-120.

Source : MNHN, Paris

Sexual Selection in Savanna Millipedes: Products, Patterns and Processes

Steven R. TELFORD * & *John Mark DANGERFIELD* **

* Department of Zoology, University of Pretoria, Pretoria 0002, South Africa
* Department of Biology, University of Botswana, P. Bag 0022, Gaborone, Botswana

ABSTRACT

The polygynandrous mating systems of savanna millipedes are a dynamic combination of simple effective male mating tactics, male behaviours that protect their reproductive investment in females and possibly female choice of high quality males. Sexual selection has led to the evolution of dimorphic characters that aid in courtship and mate acquisition. Differential development between the sexes at the onset of breeding activity leads to changes over the breeding season in the OSR, and a prevalence of alternative male mating tactics. Selection via sperm competition may be responsible for the evolution of diverse and complex male gonopods (BARNETT & TELFORD, this volume) and behaviours such as prolonging the duration of copulation. For a morphologically simple and conservative class of invertebrates, millipedes offer great potential for the study of sexual selection.

RÉSUMÉ

Sélection sexuelle chez les Diplopodes de savane : résultats, modalités et processus.

Les modes polygynandres d'accouplement chez les diplopodes de savane constituent une combinaison dynamique des tactiques d'accouplement simples et efficientes des mâles, des comportements des mâles protégeant leur investissement reproducteur auprès des femelles et d'un choix possible des femelles pour des mâles de grande qualité. La sélection sexuelle a conduit à l'évolution de caractères dimorphiques facilitant les parades et l'accouplement. Le développement différentiel entre les sexes à l'approche de la phase d'activité de reproduction conduit à des modifications de la sex-ratio opérationnelle durant la saison de reproduction et avantage les tactiques alternatives d'accouplement des mâles. La sélection par la compétition pour le sperme peut être responsable de l'évolution de gonopodes mâles complexes et diversifiés (BARNETT & TELFORD, ce volume), ainsi que de comportements tels que celui de prolonger la durée de copulation. Pour une classe d'invertébrés à morphologie simple et conservatrice, les diplopodes offrent un large potentiel de recherche dans le domaine de la sélection sexuelle.

INTRODUCTION

For most higher organisms, males produce a surplus of cheap gametes capable of fertilising an infinite number of females, while females produce a finite number of expensive gametes that require only a single mating for effective fertilisation (BATEMAN, 1948; WILLIAMS, 1966). Because of this disparity in the cost of gamete production, males display indiscriminate mating tactics, mate frequently and compete intensely with rivals, while females often exercise highly selective mate choice.

TELFORD, S. R. & DANGERFIELD, J. M., 1996. — Sexual selection in savanna millipedes: products, patterns and processes. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 565-576. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

This fundamental behavioural difference between the sexes is the source of a selective process described by DARWIN (1871) as sexual selection. Sexual selection acts on both behavioural and morphological traits that confer a mating advantage to individuals with the most elaborate variant of the trait. Sexual selection acts in two ways: competition between males for access to females (intrasexual selection); competition between males, usually via display, to be chosen by females (intersexual selection). One or both forms of selection are assumed to be responsible for the evolution of the bright and often elaborate plumage of male birds and the horns and antlers of antelope and deer (DARWIN, 1871; TRIVERS, 1985) as well as numerous other examples of pronounced sexual dimorphism (e.g. ALEXANDER *et al.*, 1979; EBERHARD, 1985). Recently, PARKER (1970) described a form of indirect intrasexual selection, namely sperm competition, in which the sperm of different males compete to fertilise ova from within the female. This process of ejaculate competition has proved to be widespread in both vertebrates (BIRKHEAD & HUNTER, 1990; BIRKHEAD, 1989; GOMENDIO & ROLDAN, 1993) and invertebrates (PARKER, 1970; WALKER, 1980; THORNHILL & ALCOCK, 1983; WAAGE, 1986) with polygynandrous mating systems.

Over the past ten years much research has focused on teasing apart the relative contributions of these selective processes to the evolution of mating systems in general (EMLEN & ORING, 1977; BORGIA, 1979), and more specifically to understanding what determines variation in male and female mating success (BROWN, 1988; CLUTTON BROCK, 1988; GRAFEN, 1988).

The study of animal mating systems aims to describe who mates with who, how often, and why. More specifically, researchers wish to identify the selective pressures responsible for the evolution of sexual dimorphism and differences in behaviour (product), determine potential morphological and behavioural correlates of variation in mating success (pattern), and identify the tactics of mate acquisition and the degree of competition therein (process). In this paper we summarise our work to date on the mating systems of southern African savanna millipedes using the themes of product, pattern, and process. We highlight aspects of the work which deserves further consideration and suggest future directions for the study of millipede mating systems.

PRODUCTS

Morphology

Southern African juliform millipedes display marked sexual dimorphism, with females typically heavier and wider, but not longer than their conspecific male counterparts (TELFORD & DANGERFIELD, 1990, 1993a, b). The ovaries of females are paired structures housed in a common median ovitube that runs from ring 15 to the last podous ring (see BLOWER, 1985; HOPKIN & READ, 1992). Our measures of clutch size for savanna millipedes range from 200-800 ova over a size range of 1.0-20.0 grams (n = 15 species, unpublished data).

A cylindrical body plan is a unifying feature of juliform millipedes. The volume of a cylinder is calculated as: $h.\pi r^2$, where h is the height of the cylinder (body length) and r the radius. If, for example, selection for increased fecundity resulted in a twofold increase in radius the resultant increase in volume could only be matched through a fourfold increase in length. The energetic costs associated with increasing body diameter are probably less than would be associated with increasing body length. Presumably natural selection has acted on female body volume in this way to accommodate the ovary and maximise the number of eggs it can contain.

Body volume is not the only sexually dimorphic character. Millipede legs are longer and broader in males compared to females and have adhesive pads on the tarsal segments. The evolution of this sex difference in morphology probably relates to courtship and copulation (see HOPKIN & READ, 1992). Our observations have shown that males of all taxa (except members of the genera *Calostreptus* and *Chersastus*) walk along the back of the female prior to engaging in copulation. The longer broader legs of males with their adhesive pads presumably aid in this

Source : MNHN, Paris

manoeuvreing and may also function in stimulating sexual receptivity in females. Both natural and sexual selection may have contributed to the evolution of sexual dimorphism in limb structure. Data on sexual dimorphism in *Alloporus uncinatus* together with the probable sources of selection are summarised in Table 1.

TABLE 1. — Sexual dimorphism in *Alloporus uncinatus*. Leg width measured in micrometer units. Significance levels: ***P<0.001, **P<0.01. N.S. = Natural Selection; S.S. = Sexual Selection. Source: Modified from TELFORD & DANGERFIELD (1990).

	Males	Females	t-test	n	Selective Pressure
Body mass (g)	8.0 ± 0.11	8.7 ± 0.13	-4.25***	110	N.S.
Body length (mm)	114.1 ± 0.65	110.7 ± 0.87	3.16**	110	N.S.\S.S.
Body width (mm)	8.9 ± 0.06	9.5 ± 0.08	-6.41***	110	N.S.
Leg length (mm)	5.9 ± 0.10	4.9 ± 0.80	-7.83***	20	S.S.
Leg width (µm)	15.9 ± 0.16	13.4 ± 0.26	-8.18***	20	S.S.

In many sexually dimorphic species, males are typically the larger sex because sexual selection favours larger males for their superior competitive ability in contests with rivals (THORNHILL & ALCOCK, 1983; TRIVERS, 1985). Body design in male millipedes may reflect their greater mobility. Mobility seems to be an important determinant of mate acquisition (see Behaviour section below) with both longer legs and longer body resulting in males being able to move more quickly and efficiently than females. This idea remains to be tested.

TABLE 2. — Sex differences in the behaviour of three species of juliform millipede expressed as the percentage of the total number of observations (values in brackets). Expected frequencies for between sex comparisons are based on the overall sex ratio for the species and the total number of observations in the behaviour category. Source: modified from DANGERFIELD, MILNER & MATTHEWS, (1992).

	Walking	Feeding	Resting	Copulating
Calostreptus carinatus				
males (62)	64.5	11.3	9.7	14.5
females (223)	25.1	34.1	36.8	4.0
χ^2	22.0***	8.6**	10.9***	8.4*
Chaleponcus digitatus				
males (148)	66.2	23.0	10.1	0.7
females (212)	34.9	42.0	22.6	0.5
χ^2	17.5***	9.7**	7.9**	0.1ns
Alloporus uncinatus				
males (86)	69.8	18.6	3.5	8.1
females (158)	47.5	40.5	7.6	4.5
χ^2	4.9*	7.9**	2.6ns	1.3ns

Source : MNHN, Paris

Behaviour

Savanna millipedes are surface active during the summer wet season and, depending on habitat and rainfall patterns, may remain active for as long as six months (DANGERFIELD & TELFORD, 1991; DANGERFIELD, MILNER & MATTHEWS, 1992; TELFORD & DANGERFIELD, 1993a). During this period adults, intercalary males and juveniles emerge from underground to feed and reproduce. Significant differences between the sexes are apparent in the time invested in the performance of these behaviours as well as in their general activity patterns (Table 2). For example, in a population of *Alloporus uncinatus* from Mazowe, Zimbabwe (17°30'S, 30°57'E) males were more active than females, who spent more time feeding in aggregates, and climbing vegetation; apparently to avoid interference from the more mobile mate-seeking males (DANGERFIELD & TELFORD, 1992; TELFORD & DANGERFIELD, 1993a). In a small patch of *Acacia* savanna in Gaborone, Botswana (24°40'S, 25°52'E) there were significant differences between the sexes of three species in time spent walking, feeding, resting and copulating (Table 2, and see DANGERFIELD, MILNER & MATTHEWS, 1992).

Males tend to be the more mobile sex and invest most of their time searching the habitat for females. Females invest more time in feeding, probably to repay their significant energetic investment in ova.

PATTERNS

Mating patterns

Correlating variation in mating success with some measure of behaviour or morphology is the standard protocol for detecting patterns of non-random mating (e.g. PARTRIDGE & HALLIDAY, 1984). Non-random mating is assumed to be the consequence of some process of sexual competition in which individuals of superior competitive ability gain a mating advantage over rival conspecifics.

In a study of mating patterns in the Mazowe population of *Alloporus uncinatus* over a single breeding season (November 1988 - May 1989) mating was random with respect to body mass (g): unmated males (mean $\pm$ 1 s.e.) = 8.16 $\pm$ 1.08, n = 868; mated males = 8.24 $\pm$ 1.05, n = 295. MANN-WHITNEY U-test: U = -1.2, P>0.1, and see Fig. 2 in TELFORD & DANGERFIELD (1993a). A lack of any significant correlations between various measures of the body sizes (mass, length, width, head width) of males and females in copula pairs supported this conclusion (see Fig. 1). However, this evidence for random mating is not conclusive as the sampling protocol did not take into account the mating histories of individuals over the duration of the breeding season. This highlights the problems of studying mating success in natural populations of small, highly abundant, inconspicuous organisms. The focus of such studies must be at the level of the individual and requires the use of effective, reliable marking techniques.

The operational sex ratio

Another powerful predictor of local mate competition is the operational sex ratio (OSR), which is the ratio of sexually receptive males to females (EMLEN & ORING, 1977). Under male biased OSR conditions males are limited in their access to females and must compete for females as a limiting resource. The reverse is true under female biased OSR conditions.

Savanna millipede communities are characterized by large-scale temporal variation, and sex differences, in emergence and activity patterns (DANGERFIELD & TELFORD, 1991; DANGERFIELD, MILNER & MATTHEWS, 1992) with the nett effect of changing OSR conditions over the breeding season.

Source : MNHN, Paris

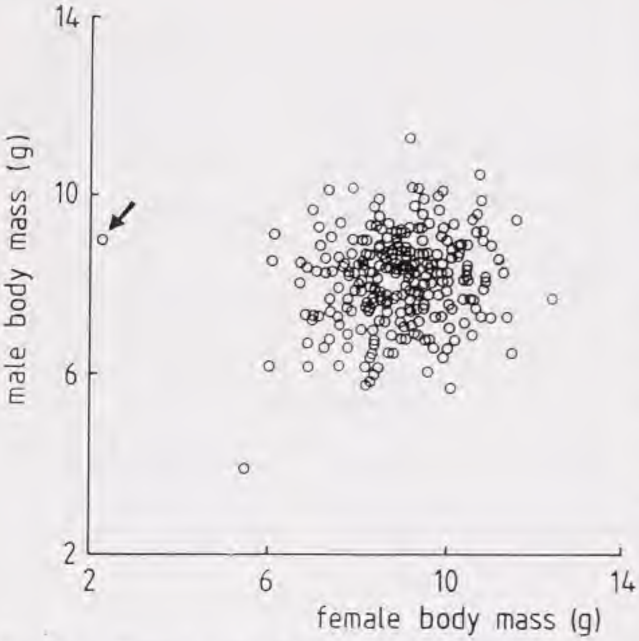


FIG. 1. — The relationship between body mass (g) of males and females in all mated pairs of *Alloporus uncinatus* collected over a single breeding season. Arrow indicates a pair in which the female received a fatal injury. Source: TELFORD & DANGERFIELD, 1993a.

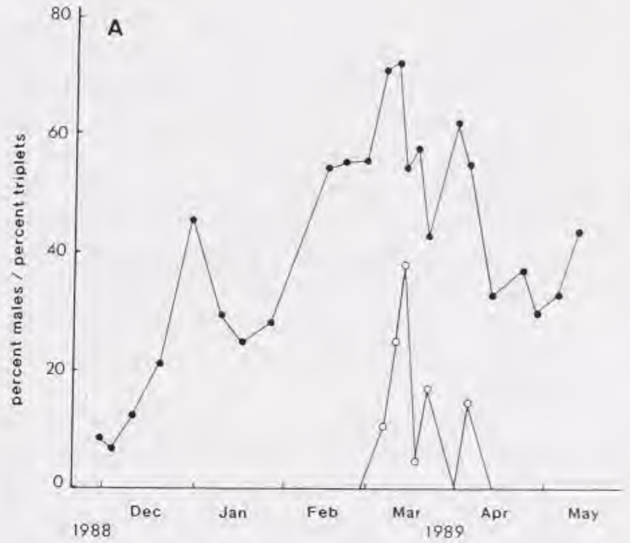


FIG. 2a. — Seasonal change in the operational sex ratio (●) and the occurrence of triplet associations as a proportion of the number of mated pairs (○) for the Mazowe population of *Alloporus uncinatus*. Source: modified from TELFORD & DANGERFIELD, 1993a.

The magnitude and timing of change in the OSR varies between populations and is also dependent on the duration of the breeding season. For example, in the Mazowe population of *A. uncinatus* the OSR was female biased at the onset of breeding. This bias gradually declined, ending in a peak of male bias coincident with the major peak in mating activity and the appearance of an alternative male mating tactic (Fig. 2a, and see TELFORD & DANGERFIELD, 1993a). This process of change in the OSR is a consequence of the presence of large numbers of intercalary males early in the season, and the gradual decline in number of mature females who presumably burrowed back into the soil to lay egg clutches.

Botswana populations of *A. uncinatus, Calostreptus carinatus* and *Chaleponcus digitatus* showed similar though less predictable change in the OSR (Fig. 2b). In a millipede community at Richards Bay, Natal (28°37'E, 32°17'S) females of the dominant species *Chersastus sanguinipes* were present constantly, but males only appeared immediately after a rainfall event, stayed for 2-3 days and then disappeared. Copula pairs were only observed during the times when males were present (Rudi VAN AARDE, pers. comm.).

In millipede breeding populations, the co-occurrence of alternative male mating tactics is a common observation under male biased OSR conditions. Instead of always searching for single females, males often joined copula pairs to form triplet associations. This observation will be discussed further in the following section.

PROCESSES

Mating experiments

Separating the effects of male-male competition from female choice remains one of the major challenges to students of sexual selection (see for example, KIRKPATRICK, 1982; ARNOLD, 1983; PARTRIDGE, 1983). Previously we argued that our field data on mating patterns were insufficient to refute

Source : MNHN, Paris

the occurrence of non-random mating.

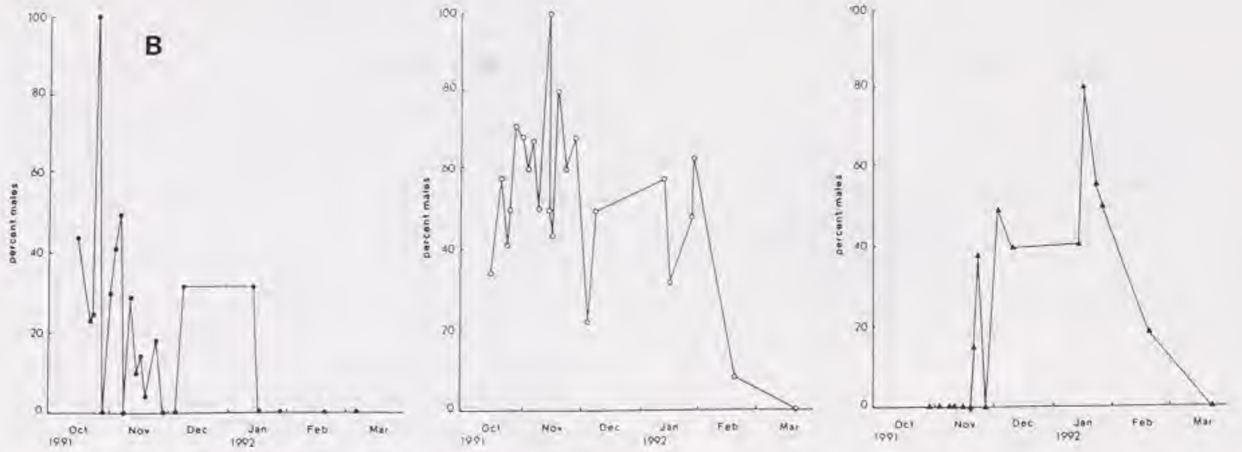


FIG. 2b. — Seasonal change in the OSR for Botswana populations of *Alloporus uncinatus* (•) *Calostreptus carinatus* (▲) and *Chaleponcus digitatus* (○).

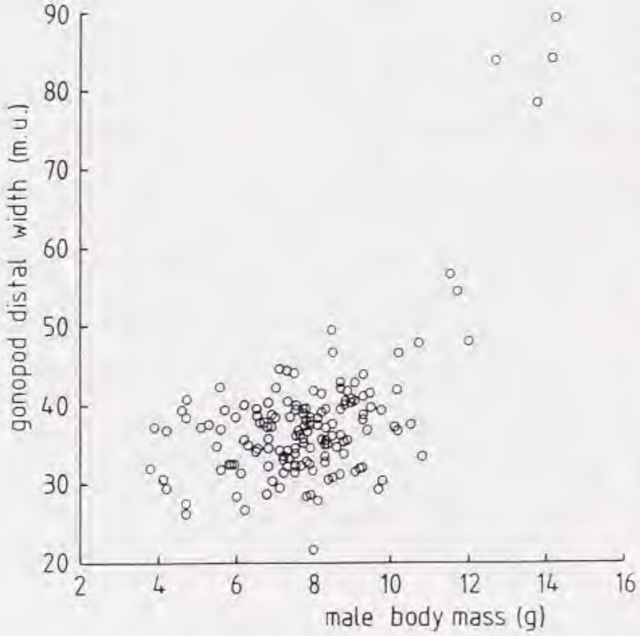


FIG. 3. — The relationship between body mass (g) and gonopod distal width for a sample of male *Alloporus uncinatus* from Mazowe.

Here we summarise results from controlled laboratory mating experiments designed to test for size assortative and size selective mating, and separate the effects of inter and intra-sexual selection in generating these mating patterns (TELFORD & DANGERFIELD, 1993b). Sequential choice experiments were conducted with *Alloporus uncinatus, Calostreptus carinatus, Spinotarsus tenuis, Chaleponcus digitatus* and *Chaleponcus limbatus.* Individual male and female mating histories for *A. uncinatus* from Mazowe (Fig. 3) and the two species of *Chaleponcus* revealed that, in the absence of a choice situation, mating was size selective (Table 3) and best explained by female choice (TELFORD & DANGERFIELD, 1993a, b). In the other species and populations mating was random.

In multiple choice mating experiments a wide variety of outcomes were observed (Table 4) including size assortative and random mating, and a mating advantage for both large and small males. In addition, between population comparisons of mating pattern were not always consistent. Our results suggest that both processes of sexual competition operate in millipede mating systems but do not always correspond for geographically separate populations of the same species (Table 5). These results should viewed as a source of testable *a priori* predictions about between-species and between-population differences in the competitive processes that generated these observed mating patterns.

Source : MNHN, Paris

TABLE 3. — Regression statistics for the relationship between frequency of acceptance and male body mass (g) for males in sequential choice mating experiments. Source: TELFORD & DANGERFIELD (1993b).

			Regression statistics		
Species	Population	Sample size	intercept	slope	r
A. uncinatus	Mazowe	245	-6.10	0.77	0.503***
	Hwange	22	-0.43	0.49	0.212ns
Calostreptus carinatus	Hwange	28	2.50	0.78	0.054ns
	Sengwa	39	1.93	1.48	0.095ns
Chaleponcus limbatus	V. Falls	35	-5.54	8.60	0.500**
	Marondera	25	-5.43	5.14	0.677***
Chaleponcus digitatus	Marondera	19	-8.77	8.77	0.583**
Spinotarsus	Marondera	16	2.06	0.42	0.001ns

TABLE 4. — Acceptance by females of first, second and third rank males as first and second mating partners in multiple choice mating experiments and the proportion of females that accepted a second male (PA). Source: modified from TELFORD & DANGERFIELD (1993b).

Species	Population		1st rank males	2nd rank males	3rd rank males	χ^2	PA
A. uncinatus	Mazowe	1st	15	7	3	7.85*	
		2nd	0	0	0	na	0
		2nd	6	2	4	2.00ns	48
Calostreptus carinatus	Hwange	1st	2	5	3	1.40ns	
		2nd	2	0	2	2.00ns	40
	Sengwa	1st	4	1	8	5.60*	
		2nd	2	1	3	1.00ns	46
Chaleponcus limbatus	V. Falls	1st	6	4	3	1.08ns	
		2nd	0	0	0	na	0
	Marondera	1st	7	2	1	6.19*	
		2nd	0	0	0	na	0
Chaleponcus digitatus	Marondera	1st	11	34	6.37*		
		2nd	4	1	5	2.48ns	50
Spinotarsus tenuis	Marondera	1st	7	1	1	8.00**	
		2nd	1	2	0	1.00ns	33
Spinotarsus cuspidosus	Marondera	1st	9	40		9.39**	
		2nd	0	0	0	na	0

Source : MNHN, Paris

MATING TACTICS

Intrasexual competition

Observations of courtship and copulation as well as mate seeking behaviour in both the field and laboratory provide further insight into the tactics of mate acquisition and processes of sexual competition employed by millipedes. Competition between males can be both direct and indirect. The primary mating tactic appears to be a scramble for mates in which males seek females through a random search of the habitat (TELFORD & DANGERFIELD, 1993a). When conspecifics are encountered males attempt copulation and tend to be indiscriminate. Interindividual differences in time spent searching and speed of movement may generate variance in male mating success and is, therefore, a form of indirect competition. Under male biased OSR conditions single males often join with copula pairs to form triplet associations (Fig. 2a, and see TELFORD & DANGERFIELD, 1990, 1993a) and either wait for the pair to separate before attempting to mate with the female (Spirostreptidae) or actively attempt to displace the copulating male (Odontopygidae). Attempted displacement of copulating males is a common mating tactic in invertebrate and anuran mating systems (THORNHILL & ALCOCK, 1983; LAMB, 1984; TELFORD & VAN SICKLE, 1990) and is a form of direct male competition.

Why males switch from searching for single females to associating with copula pairs when the OSR is male biased is an interesting unanswered question. We suggest that this change in behaviour does not reflect inferior competitive ability; as is the case for males of many species that perform alternative mating tactics (KREBS & DAVIES, 1987). A more parsimonious explanation is that as the OSR becomes increasingly male biased, encounter frequency with solitary females declines. Males then simply associate with the first female they meet regardless of whether she is paired or alone. This behaviour is "tolerated" by copulating males because they would have to release the female in order to repel the other male. One reason for this apparent tolerance of copulating males is because the physical nature of copulation (TELFORD & WEBB, in prep.) together with its long duration under male control (TELFORD & DANGERFIELD, 1993b, c) creates a potential sexual conflict of interest in which the male stands to gain more than the female.

Prolonged copulation is advantageous for males because it protects their reproductive investment in females under conditions of intense intrasexual competition (TELFORD & DANGERFIELD, 1991). The potential evolutionary benefits to females are less obvious (see THORNHILL & ALCOCK, 1983). Females can incur physical damage during copulation (see Fig. 1) which may be compounded through multiple mating (see for example, FOWLER & PARTRIDGE, 1989). Therefore, if a male releases a female to repel a rival male she may become unwilling to resume copulation. However, this still begs the question of why females remate with the second male in triplet associations. While the evolutionary benefits a male enjoys from multiple mating are obvious and well documented the same is not true for females (THORNHILL & ALCOCK, 1983). An often argued potential benefit of multiple mating by females is the increased heterozygosity in their offspring; this prediction still lacks empirical verification.

Copulation in spirostreptid millipedes occurs either in parallel (*Calostreptus*), head to head (*Rhodesiostreptus matabele),* or with the male coiled around the female (TELFORD & DANGERFIELD, 1990, 1993b). Interestingly, parallel copulators tend to mate for a shorter time period than coiled copulators. *Chaleponcus* sp. has the shortest copulation duration for a coiled copulator and single males of this species actively attempt to displace copulating males. However, attempted displacement has never been observed in parallel copulators which also typically perform short duration copulations. The significance of between species variation in copulation duration remains unclear, and definately warrants further study. Data on copulation

Source : MNHN, Paris

position, duration and displacement, copulatory guarding, and triplet formation are summarised in Table 6.

TABLE 5. — Predictions of expected mating patterns and processes of sexual competition in the mating systems of nine populations of spirostreptid millipede. Predictions are based on results obtained from sequential and multiple choice mating experiments (tables 3 & 4). * Small male mating advantage. ♂-♂ Comp.= male-male competition.

Species	Population	Sequential Choice		Multiple Choice	
		Pattern	Process	Pattern	Process
A. uncinatus	Mazowe	Size-Selective	♀ Choice	Size-Selective	♀ Choice ♂-♂ Comp.
	Hwange	Random	-	Size-Assortative	♀ Choice
Calostreptus carinatus	Hwange	Random	-	Size-Assortative	♀ Choice
	Sengwa	Random	-	Size-Selective*	♀ Choice
Chaleponcus limbatus	V. Falls	Size-Selective	♀ Choice	Random	-
	Marondera	Size-Selective	♀ Choice	Size-Selective	♀ Choice ♂-♂ Comp.
Chaleponcus digitatus	Marondera	Size-Selective	♀ Choice	Size-Selective	♀ Choice ♂-♂ Comp.
Spinotarsus tenuis	Marondera	Random	-	Size-Selective	♀ Choice ♂-♂ Comp.
Spinotarsus cuspidosus	Marondera	-	-	Size-Selective	♀ Choice ♂-♂ Comp.

Prolonged copulation in invertebrates appears to have evolved as a form of mate guarding in which males protect their reproductive investment in females by limiting their opportunity to remate (see THORNHILL & ALCOCK, 1983). In *Alloporus uncinatus,* males alter the duration of copulation according to predictions of the mate-guarding hypothesis (TELFORD & DANGERFIELD, 1993 b, c). Sperm competition (*sensu* PARKER, 1970) is the most likely process responsible for selection favouring the evolution of this form of mate guarding by males. This may also be true for other species of millipede with prolonged copulation (see Table 6).

Intersexual competition

In some invertebrates, primary or accessory genitalia scale positively with body size (EBERHARD, 1985; unpublished data for eight species of spirostreptid millipedes). In libellulid dragonflies, the hook-like structures at the end of the penis scale positively with body size and both size and degree of symmetry correlate with sperm volumes removed (MILLER, 1991). EBERHARD (1985) has suggested that females could use such a scaling relationship as a cue to male body size and use the information to choose large males as mates. We have already suggested that female choice may partially explain the mating advantage enjoyed by large males

Source : MNHN, Paris

of several species in sequential and multiple choice mating experiments (Table 5). However, invoking genitalic scaling as the mechanism of female choice may be incorrect.

For example, although the gonopods of *A. uncinatus* scale positively with body size (Fig. 3), the sizes of males and females in copula pairs from Mazowe do not correlate. If females do choose males on this basis then we would predict a positive relationship between the size of mating partners, or a correlation between mating success and body size in natural populations. To more fully understand this potential mechanism of female choice requires a systematic study of the ultrastructure of male and female genitalia (see BARNETT & TELFORD, this volume) together with a study of mating patterns in populations of known individuals.

TABLE 6. — Copulation duration in minutes (mean ± 1 s.d.) for eight populations of spirostreptid millipede (sample sizes are given in brackets). Copula positions are given below species names. Source: modified from TELFORD & DANGERFIELD (1993b), and unpublished data.

Family / Species	Population	Copulation duration	Triplets (Y/N)	Displacement (Y/N)
Spirostreptidae				
Alloporus uncinatus (coiled)	Mazowe	122.7 ± 49.4 (35)	Y	N
	Hwange	205.8 ± 60.8 (25)	Y	N
Calostreptus sp. (parallel)	Hwange	60.3 ± 25.6(22)	N	N
	Sengwa	33.8 ± 22.9 (25)	N	N
Odontopygidae				
Chaleponcus sp.1 (coiled)	Marondera	22.6 ± 17.9 (40)	Y	Y
Chaleponcus sp.3 (coiled)	V. Falls	80.2 ± 25.3 (20)	Y	Y
	Marondera	85.6 ± 16.6 (19)	Y	Y
Chaleponcus digitatus (coiled)	Marondera	66.0 ± 11.2 (28)	Y	N
Spinotarsus tenuis (coiled)	Marondera	92.3 ± 18.6 (19)	Y	?

CONCLUSIONS

Millipedes are a conspicuous group of organisms, present in a wide variety of habitats and typically occurring at high population densities. They adapt well to laboratory conditions and are useful subjects for experimental manipulation.

Our study of the mating system of *Alloporus uncinatus* over a single breeding season revealed the nature of male mating tactics, the impact of change in the OSR on male mating tactics, and the role of stochasticity in generating the observed mating pattern. Our comparative data from laboratory mating experiments suggests that both male competition and female choice shape mating systems and that the relative roles of the two processes can differ between populations of the same species. Between population plasticity in mating systems is believed to be a consequence of the combined effects of environmental variability, differing population densities and operational sex ratios. Together, these results and predictions can be used to generate *a priori* hypotheses about plasticity in millipede mating systems, testable through detailed longitudinal studies of natural populations.

Source : MNHN, Paris

Descriptive studies, for example between species variation in the duration of copulation, are a necessary starting point for the investigation of the adaptive significance of any behaviour pattern. We have shown experimentally, that in *A. uncinatus* prolonging the duration of copulation is a form of mate guarding (TELFORD & DANGERFIELD, 1991) and our comparative data allow us to make similar predictions for other species. Where copulation duration is not prolonged the mate guarding explanation does not hold but nevertheless makes way for alternative *a priori* predictions to be made. For example, if copulation duration is short it may be because female remating frequency is low. Therefore, selection to guard females is relaxed and a better tactic for males is to reduce time spent in copula and maximise mating frequency.

The data presented here confirm the polygynandrous nature of savanna millipedes which, together with the capacity of females to store sperm and the functional role of gonopods in sperm displacement (BARNETT & TELFORD, this volume), highlight the importance of sperm competition in millipede mating systems. Quantifying sperm precedence patterns is essential to a complete understanding of the relative contributions of different processes of sexual competition to observable variation in male and female mating success.

REFERENCES

ALEXANDER, R. D., HOOGLAND, J. L., HOWARD, R. D., NOONAN, K. M. & SHERMAN, P. W., 1979. — Sexual dimorphism and breeding systems in pinnipeds, ungulates, primates and humans. *In* : N. A. CHAGNON & W. IRONS, *Evolutionary biology and human social behaviour: An anthropological perspective.* North Scituate.

ARNOLD, S. J., 1983. — Sexual selection: The interface of theory and empiricism. *In* : P. BATESON, *Mate Choice* . Cambridge, Cambridge University Press : 67-108.

BARNETT, M., TELFORD, S. R. & DE VILLIERS, C. J., 1993. — Sperm displacement in a millipede? - an investigation into the genital morphology of the southern African Spirostreptid millipede *Orthoporus pyrhocephalus*. *J. Zool. Lond.*, **3** : 511.

BATEMAN, A. J., 1948. — Intrasexual selection in *Drosophila. Heredity*, **2** : 349-368.

BIRKHEAD, T. R., 1989. — The intelligent sperm? A concise review of sperm competition. *J. Zool. Lond.*, **218** : 347-351.

BIRKHEAD, T. R. & HUNTER, F. M., 1990. — Mechanisms of sperm competition. *Trends Ecol. Evol.*, **5** : 48-52.

BOAKE, C. R. B., 1986. — A method for testing adaptive hypotheses of mate choice. *Am. Nat.*, **127** : 654-666.

BORGIA, G., 1979. — Sexual selection and the evolution of mating systems. *In*: N. S. BLUM & M. A. BLUM, *Sexual selection and reproductive competition in insects.* New York, Academic Press.

BLOWER, J. G., 1985. — Millipedes. [*In* : D. M. KERMACH & R. S. K. BARNES, *Synopses of the British Fauna.*, **35**], London, E. J. Brill. & W. Backhuys, 242 pp.

BROWN, D., 1988. — Components of Lifetime Reproductive Success. *In* : T. H. CLUTTON BROCK, *Reproductive Success.* Chicago, University of Chicago Press : 439-453.

CLUTTON BROCK, T. H., 1988. — Reproductive Success. In: T. H. CLUTTON BROCK, *Reproductive Success.* Chicago, University of Chicago Press : 472-485.

DANGERFIELD, J. M. & TELFORD, S. R., 1991. — Seasonal activity patterns of Julid millipedes in Zimbabwe. *J. Trop. Ecol.*, **7** : 281-285.

DANGERFIELD, J. M. & TELFORD, S. R., 1992. — Species diversity of Juliform millipedes: Between habitat comparisons within the seasonal tropics. *Pedobiologia* , **36** : 321-329.

DANGERFIELD, J. M., MILNER, A. E. & MATTHEWS, R., 1992. — Seasonal activity patterns and behaviour of juliform millipedes in south-eastern Botswana. *J. Trop. Ecol.*, **8** : 451-464.

DARWIN, C., 1871. — *The descent of man and selection in relation to sex.* London, John Murray.

EBERHARD, W. G., 1985. — *Sexual selection and animal genitalia.* Cambridge: Harvard University Press.

EMLEN, S. T. & ORING, L. W., 1977. — Ecology, sexual selection and the evolution of mating systems. *Science* , **197** : 215-223.

FOWLER, K. & PARTRIDGE, L., 1989. — A cost of mating in female fruitflies. *Nature* , **338** : 760-761.

GRAFEN, A., 1988. — On the uses of Data on Lifetime Reproductive Success. *In* : T. H. CLUTTON BROCK, *Reproductive Success.*. Chicago, University of Chicago Press : 454-471.

GOMENDIO, M. & ROLDAN, E. R. S., 1993. — Mechanisms of sperm competition: Linking physiology and behavioural ecology. *Trends Ecol. Evol.*, **8** : 95-100.

Source : MNHN, Paris

HOPKIN, S. P. & READ, H. J., 1992. — *The biology of millipedes.* Oxford, Oxford Univ. Press, 233 pp.

KIRKPATRICK, M., 1982. — Sexual selection and the evolution of female choice. *Evolution*, **36** : 1-12.

KREBS, J. R. & DAVIES, N. B., 1987. — *An introduction to behavioural ecology.* Oxford, Blackwell Scientific Publications.

LAMB, T., 1984. — Amplexus displacement in the southern toad *Bufo terrestris*. *Copeia* : 1023-1025.

MILLER, P. L., 1991. — The structure and function of the genitalia in the Libellulidae (Odonata). *Zool. J. Linn. Soc.*, **102** : 43-73.

PARKER, G. A., 1970. — Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.*, **45** : 525-567.

PARTRIDGE, L., 1983. — Non random mating and offspring fitness. *In* : P. BATESON, *Mate Choice*. Cambridge, Cambridge University Press : 67-108.

PARTRIDGE, L. & HALLIDAY, T. R., 1984. — Mating patterns and mate choice. *In* : J. R. KREBS & N. B. DAVIES, *Behavioural ecology: An evolutionary approach*. Oxford, Blackwell Scientific Publications : 222-250.

TELFORD, S. R. & DANGERFIELD, J. M., 1990. — Sex in millipedes: laboratory experiments on sexual selection. *J. Biol. Ed.*, **24** : 233-238.

TELFORD, S. R. & DANGERFIELD, J. M., 1991. — Sex ratio manipulation and copulation duration in the tropical millipede, *Alloporus uncinatus*: A test of the copulatory guarding hypothesis. *Anim. Behav.*, **40** : 984-986.

TELFORD, S. R. & DANGERFIELD, J. M., 1993a. — Mating tactics in the tropical millipede *Alloporus uncinatus* (Diplopoda; Spirostreptidae). *Behaviour*, 124 : 45-57.

TELFORD, S. R. & DANGERFIELD, J. M., 1993b. — Mating behaviour and mate choice experiments in some tropical millipedes (Diplopoda: Spirostreptidae). *S. A. J. Zool.*, **28** :155.

TELFORD, S. R. & DANGERFIELD, J. M., 1993c. — Males control the duration of copulation in the tropical millipede, *Alloporus uncinatus*. *S. A. J. Zool.*, 29 : 266.

TELFORD, S. R. & VAN SICKLE, J., 1989. — Sexual selection in an African toad (*Bufo gutteralis*): The roles of morphology, amplexus displacement and chorus participation. *Behaviour*, **110** : 62-75.

THORNHILL, R. & ALCOCK, J. 1983. — *The evolution of insect mating systems.* Cambridge, Massachusetts, Harvard University Press.

TRIVERS, R. L., 1972. — Parental investment and sexual selection. *In* : B. CAMPBELL, *Sexual Selection and the Descent of Man.* Chicago, Aldine : 136-179.

WAAGE, J. K., 1986. — Evidence for widespread sperm displacement ability among Zygoptera (Odonata) and the means for predicting its presence. *Biol. J. Linn. Soc.*, **28** : 285-300.

WALKER, W. F., 1980. — Sperm utilisation strategies in nonsocial insects. *Am. Nat.*, **115** : 780-799.

WILLIAMS, G. C., 1966. — *Adaptation and Natural Selection.* Princeton, NJ, Princeton University Press.

Source : MNHN, Paris

Trophic Preferences of Three Soil Macroarthropods (Preliminary Study)

Jorge P. CANCELA DA FONSECA *& Leïla* MEZIANE

Analyse des Systèmes Écologiques, Écologie du Sol, C.N.R.S.
Université Paris 7, Laboratoire de Biologie végétale et d'Écologie forestière, F-77300 Fontainebleau, France

ABSTRACT

The main objective of this study is to compare the trophic behaviour of two macroarthropod species belonging to two different invertebrate groups - Diplopoda and Isopoda - but which are, apparently, morphologically similar and have a similar defence, armadillo behaviour (roller species): *Glomeris marginata* (Villers) and *Armadillidium vulgare* (Latreille). *Oniscus asellus* Linné, a clinger species, was also taken into account. These species coexist in the soil of Fontainebleau and Montmorency Forests. They feed on beech, oak and chestnut litter. Three classes of leaf litter were tested out: I. Litter of the year; dark leaves, thick, with few or no rotting spots; II. Old litter; dark leaves, thick but thinner than in I., with light rotting spots; and, III. Old litter; bleached, thin leaves. A Student-t test of the data shows that the three species have a similar trophic behaviour concerning the chestnut litter, but a different one concerning the litter of both beech and oak.

RÉSUMÉ

Préférences alimentaires de trois macroarthropodes édaphiques (étude préliminaire).

Le principal objectif de cette étude est de comparer le comportement trophique de deux espèces de macroarthropodes appartenant à deux groupes différents d'invertébrés - Diplopoda et Isopoda - mais qui sont, en apparence, morphologiquement semblables et ont un comportement de défense similaire en se roulant en boule : *Glomeris marginata* (Villers) et *Armadillidium vulgare* (Latreille). *Oniscus asellus* Linné, isopode dépourvu de capacité de volvation, a été aussi pris en compte. Ces espèces coexistent dans les sols des forêts de Fontainebleau et de Montmorency. Elles se nourrissent de litière de hêtre, de chêne et de châtaignier. On a testé trois classes de litière : I. Litière de l'année ; feuilles sombres, épaisses, sans ou avec peu de taches de pourriture blanche ; II. Litière des années précédentes ; feuilles sombres, épaisses, mais plus minces qu'en I., avec des taches claires de pourriture blanche ; et, III. Litière des années précédentes ; feuilles minces, blanchies. L'application aux données du test-t de Student a montré que les individus de ces trois espèces d'arthropodes présentent un comportement trophique similaire en ce qui concerne la litière de châtaignier, mais différent vis-à-vis des litières de hêtre et de chêne.

INTRODUCTION

The main objective of this study was to compare the trophic behaviour of two soil macroarthropod species belonging to two different invertebrate groups, Diplopoda and Isopoda, but which are, apparently, morphologically similar and have a similar rolling defence, "armadillo" behaviour: *Glomeris marginata* (Villers) and *Armadillidium vulgare* (Latreille). Few studies compare these two macroarthropod species. In general, they compare either the two

---

CANCELA DA FONSECA, J. P. & MEZIANE, L., 1996. — Trophic preferences of three soil macroarthropods (Preliminary study). *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn Hist. nat.*, **169** : 577-584. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

isopods *A. vulgare* and *Oniscus asellus* Linné, or the latter species with *G. marginata* (e.g. HARTENSTEIN, 1964; NEUHAUSER & HARTENTSTEIN, 1978; HASSALL & RUSHTON, 1984; INESON & ANDERSON, 1985; SUTTON & HARDING, 1989). One of the few authors that compared these two species of isopods with one species of *Glomeris*, not *G. marginata* but *G. connexa* Koch, was DUNGER (1958). However, these three species coexist in the same ecosystem we studied several years ago, a beech woodland: La Tillaie in Fontainebleau Forest (MEZIANE, 1976; CANCELA DA FONSECA & MEZIANE, 1978). This is why *O. asellus* is also taken into account.

Our aim was to study comparatively the ecological niches of two roller species coming from two different arthropod classes (Crustacea and Diplopoda) and their differential roles on the breakdown of forest litter. For this, one of the points was to detail the trophic preferences of such species. This preliminary work presents some significant results related to litter preferences, useful for the comprehension and development of future studies dealing with comparative ecological importance of individuals and populations forming such "functionnal macroarthropod groups".

MATERIAL AND METHODS

The two roller species studied here are *A. vulgare* (AVU) and *G. marginata* (GMA), and the clinger species, *O. asellus* (OAS).

All were present in both the Fontainebleau and Montmorency Forest ground floors. They feed on litter. Three types of litter were given to them in our experiments: Beech litter (*Fagus sylvatica* Linné - FSY), Oak litter (*Quercus sessiliflora* Salisbury - QSE) and Chestnut litter (*Castanea sativa* Miller - CSA). Three classes of litter were used under the experimental conditions : I. Litter of the year, autumn 1976; dark leaves, thick, with few or no rotting spots; II. Old litter of the years before 1976; dark leaves, thick but thinner than in I., with light rotting spots; and, III. Old litter of the years before 1976; bleached, thin leaves. Five replicates were done with a number of leaves variable according to the number of leaves available in each class. The emphasis was put on the beech litter. The experiments were made at room conditions of about 15-17°C and 80% R.H. from May to November 1977. Each adult, after 48 hours with no food (fasting), was put in contact with each type of litter for a period of 2 days.

The consumption rates (in %) were evaluated by assessing the area of the leaves eaten by each adult in relation to the total leaf area available. The numerical results (Table 1, Fig. 1) were analysed by the Student-t test (Table 2).

RESULTS

First of all, the three species, but mainly the millipede *G. marginata* and the woodlouse *O. asellus*, have a clear preference to the chestnut litter (classes I, II and III), and a significant avoidance, less for *G. marginata*, of the beech litter of the year (class I). However, the most important antagonistic difference of the feeding behaviour between the millipede *G. marginata* and the woodlouse *A. vulgare* concerns the almost complete avoidance of, respectively, the oak and the beech litter of the year (class I). The same kind of opposition concerned their preferences to the old, thick beech litter (class II). In relation to *G. marginata*, *O. asellus* has a trophic behaviour similar to that of *A. vulgare*, except for the old, thick beech litter (class II).

Furthermore, *A. vulgare* seems to prefer the thick chestnut and oak litter to the beech one (classes I and II), while *G. marginata* seems to prefer the beech litter to the oak litter of the year (class I), the chestnut litter to the oak and the beech litter of the year (class I), and the old, thick chestnut litter to the old, thick beech litter (class II). *O. asellus* prefers the chestnut and the oak litter of the year to the beech one (class I), and the whole old chestnut litters to those of beech (classes II and III).

Comparing the frequency profiles of the data some "odd" data were excluded. This mainly increased the significant differences already observed. However, some significant differences appeared, but above all for the classes with rather few data.

Source : MNHN, Paris

TABLE 1. — Mean consumption rates (%) of litter classes by *Glomeris marginata*, *Armadillidium vulgare* and *Oniscus asellus*. $\bar{x}$ = Corrected means.

Tree species	Litter classes	*G. marginata*		*A. vulgare*		*O. asellus*	
		No. of leaves	$\bar{x} \pm s_{\bar{x}}$	No. of leaves	$\bar{x} \pm s_{\bar{x}}$	No. of leaves	$\bar{x} \pm s_{\bar{x}}$
F. sylvatica	I	27	36.7± 7.4	28	14.5± 4.0	24	11.8± 2.0
	Ix			25	8.0± 1.9		
	II	36	46.3± 5.8	37	29.3± 4.7	41	43.6± 4.4
	IIx			34	24.6± 3.9	39	45.8± 4.3
	III	6	27.1±15.5	8	47.8±11.8	9	53.6±10.5
	IIIx	5	13.4± 8.9	7	53.8±11.7	8	60.3± 9.1
Q. sessiliflora	I	8	7.3± 4.7	8	52.2±10.6	4	48.1± 8.7
	Ix	7	3.0± 2.1	7	58.2±10.1		
	II	11	54.2±14.3	11	52.2± 8.9	17	54.4± 7.4
	IIx	9	60.1±14.7	10	62.7± 8.6	16	57.2± 7.3
	III	6	42.6±13.8	6	51.2±15.8	3	64.3±23.1
	IIIx	5	51.1±13.3	5	60.9±15.3	2	87.3± 4.7
C. sativa	I	7	82.1± 7.3	10	56.6± 9.5	10	68.9± 9.1
	Ix			9	51.8± 8.9	9	75.7± 6.6
	II	12	78.1± 8.2	7	66.9± 9.6	4	75.8± 9.6
	IIx	11	85.2± 4.5				
	III	5	76.2±19.1	7	71.1±11.4	9	83.5± 7.6
	IIIx	4	95.3± 2.0	8	88.9± 6.1		

DISCUSSION AND CONCLUSION

In the beech woodland of "La Tillaie" (Fontainebleau Forest) of the three macroarthropod species, *A. vulgare* was dominant (72%) followed by *O. asellus* (15%) and *G. marginata* (13%) (February 1972-January 1973; MEZIANE, 1976). Their coexistence in time and space, measured in terms of "activity behaviour" by pitfall trap method, was more important for *G. marginata* and *A. vulgare* (SCHOENER's index Rt=0.636 and Rs=0.746) than for *G. marginata* and *O. asellus* (Rt=0.583 and Rs=0.604), while, for *A. vulgare* and *O. asellus*, it was somewhat higher in time (Rt=0.652) and lower in space (Rs=0.563). Their spatial distribution was also different: more random for *G. marginata* (negative binomial distribution parameter k=8.48), more aggregative for *O. asellus* (k=0.62), and for *A. vulgare* in between (k=3.21). Though the surface of the site studied was not very large, its central part was not covered by herbaceous vegetation, only by beech litter, but their peripheric borders have a great number of mesohabitats, like fallen beech trunks and branches, decayed logs, small grassy patches, several holly bushes, and a small grassland glade. Thus, as the three species were present everywhere and coexist in this site, they can easily overlap part of their ecological niches. Nevertheless, they had some habitat preferences: *G. marginata* for the uncovered litter, *O. asellus* for the decayed wood places, and *A. vulgare* for the grassy patches and the small grassland glade. It is well known that *G. marginata* prefers woodland to grassland soils where it inhabits very often with *A. vulgare*, which prefers them, and that *O. asellus* prefers woodland soils and decayed wood (WARBURG, 1968; WALLWORK, 1976; RUSHTON & HASSALL, 1983; HASSALL & RUSHTON, 1984; SUTTON & HARDING, 1989).

Source : MNHN, Paris

TABLE 2. — Significant trophic preferences between *Glomeris marginata*, *Armadillidium vulgare* and *Oniscus asellus*.
In brackets: a) Classes of litter; b) Corrected means.
Significance: n.s. = not significant; * = 0.05>P>0.01; ** 0.01>P>0.001; *** = P<0.001.

Species	Type of preferences	Consumption rates (%)	P<5%
G. marginata	.Over *A. vulgare*:		
	Thick BEECH litter of the year (I)	36.7 *vs* 14.5	*
		(36.7 *vs* 8.0	***)
	Thick, old BEECH litter (II)	46.3 *vs* 29.3	*
		(46.3 *vs* 24.6	**)
	.Over *O. asellus*:		
	Thick BEECH litter of the year (I)	36.7 *vs* 11.8	**
	.Thick BEECH litter of the year (I)	36.7 *vs* 7.3	*
	vs thick OAK litter of the year (I)	(36.7 *vs* 3.0	*)
	.Thin, old OAK litter (III)	42.6 *vs* 27.1	n.s.
	vs thin, old BEECH litter (III)	(51.1 *vs* 13.4	*)
	.Thick CHESTNUT litter of the year (I)	82.1 *vs* 36.7	**
	vs thick BEECH litter of the year (I)		
	.Thick, old CHESTNUT litter (II)	78.1 *vs* 46.3	**
	vs thick, old BEECH litter (II)	(85.2 *vs* 46.3	***)
	.Thin, old CHESTNUT litter (III)	76.2 *vs* 27.1	n.s.
	vs thin, old BEECH litter (III)	(95.3 *vs* 13.4	***)
	.Thick CHESTNUT litter of the year (I)	82.1 *vs* 7.3	***
	vs thick OAK litter of the year (I)	(82.1 *vs* 3.0	***)
	.Thin, old CHESTNUT litter (III)	76.2 *vs* 42.6	n.s.
	vs thin, old OAK litter (III)	(95.3 *vs* 51.1	*)
	.Thick, old BEECH litter (II)	46.3 *vs* 27.1	n.s.
	vs thin, old BEECH litter (III)	(46.3 *vs* 13.4	*)
	.Thick, old OAK litter (II)	54.2 *vs* 7.3	*
	vs thick OAK litter of the year (I)	(60.1 *vs* 3.0	***)
	.Thin, old OAK litter (III)	42.6 *vs* 7.3	*
	vs thick OAK litter of the year (I)	(51.1 *vs* 3.0	**)

Species	Type of preferences	Consumption rates (%)	P<5%
A. vulgare	.Over *G. marginata*:		
	Thick OAK litter of the year (I)	52.2 *vs* 7.3	***
		(58.2 *vs* 3.0	***)
	Thin, old BEECH litter (III)	47.9 *vs* 27.1	n.s.
		(53.8 *vs* 13.4	*)
	.Thick OAK litter of the year (I)	52.2 *vs* 14.5	***
	vs thick BEECH litter of the year (I)	(58.2 *vs* 8.0	***)
	.Thick, old OAK litter (II)	52.2 *vs* 29.3	**
	vs thick, old BEECH litter (II)	(62.7 *vs* 24.6	***)

Source : MNHN, Paris

A. vulgare (continued)	.Thick CHESTNUT litter of the year (I) *vs* thick BEECH litter of the year (I)	56.6 *vs* 14.5 (51.8 *vs* 8.0	*** ***)
	.Thick, old CHESTNUT litter (II) *vs* thick, old BEECH litter (II)	66.9 *vs* 29.3 (66.9 *vs* 24.6	** ***)
	.Thick, old BEECH litter (II) *vs* thick BEECH litter of the year (I)	29.3 *vs* 14.5 (24.6 *vs* 8.0	* **)
	.Thin, old BEECH litter (III) *vs* thick BEECH litter of the year (I)	47.8 *vs* 14.5 (53.8 *vs* 8.0	** ***)
	.Thin, old BEECH litter (III) *vs* thick, old BEECH litter (II)	47.8 *vs* 29.3 (53.8 *vs* 24.6	n.s. **)

Species	Type of preferences	Consumption rates (%)	P<5%
O. asellus	.Over *G. marginata*: Thick OAK litter of the year (I)	48.1 *vs* 7.3 (48.1 *vs* 3.0	** ***)
	Thin, old BEECH litter (III)	53.6 *vs* 27.1 (60.3 *vs* 13.4	n.s. **)
	.Over *A. vulgare*: Thick, old BEECH litter (II)	43.6 *vs* 29.3 (45.8 *vs* 24.6	* ***)
	.Thick OAK litter of the year (I) *vs* thick BEECH litter of the year (I)	48.1 *vs* 11.8	***
	.Thick CHESTNUT litter of the year (I) *vs* thick BEECH litter of the year (I)	68.9 *vs* 11.8 (75.7 *vs* 11.8	*** ***)
	.Thick, old CHESTNUT litter (II) *vs* thick, old BEECH litter (II)	75.8 *vs* 43.6 (75.8 *vs* 45.8	* *)
	.Thin, old CHESTNUT litter (III) *vs* thin, old BEECH litter (III)	83.5 *vs* 53.6 (88.9 *vs* 60.3	* *)
	.Thick CHESTNUT litter of the year (I) *vs* thick OAK litter of the year (I)	68.9 *vs* 48.1 (75.7 *vs* 48.1	n.s. *)
	.Thick, old BEECH litter (II) *vs* thick BEECH litter of the year (I)	43.6 *vs* 11.8 (45.8 *vs* 11.8	*** ***)
	.Thin, old BEECH litter (III) *vs* thick BEECH litter of the year (I)	53.6 *vs* 11.8 (60.3 *vs* 11.8	*** ***)
	.Thin, old OAK litter (III) *vs* thick OAK litter of the year (I)	64.3 *vs* 48.1 (87.3 *vs* 48.1	n.s. *)

Fontainebleau Forest is mainly a beech-oak forest while Montmorency Forest has also chestnut woods. This is why our experimental trophic research concerned principally beech litter and secondly oak and chestnut litter. Laboratory results showed significant trophic differences between the three macroarthropod species in relation to the consumption rates of beech and oak litter. No significant differences being observed in relation to the consumption rates of chestnut litter. Thus, the pill millipede, *G. marginata*, avoids the thick oak litter of the year (which was also observed by GEOFFROY *et al.*, 1987) more intensely than the two woodlice, *A. vulgare* and

Source : MNHN, Paris

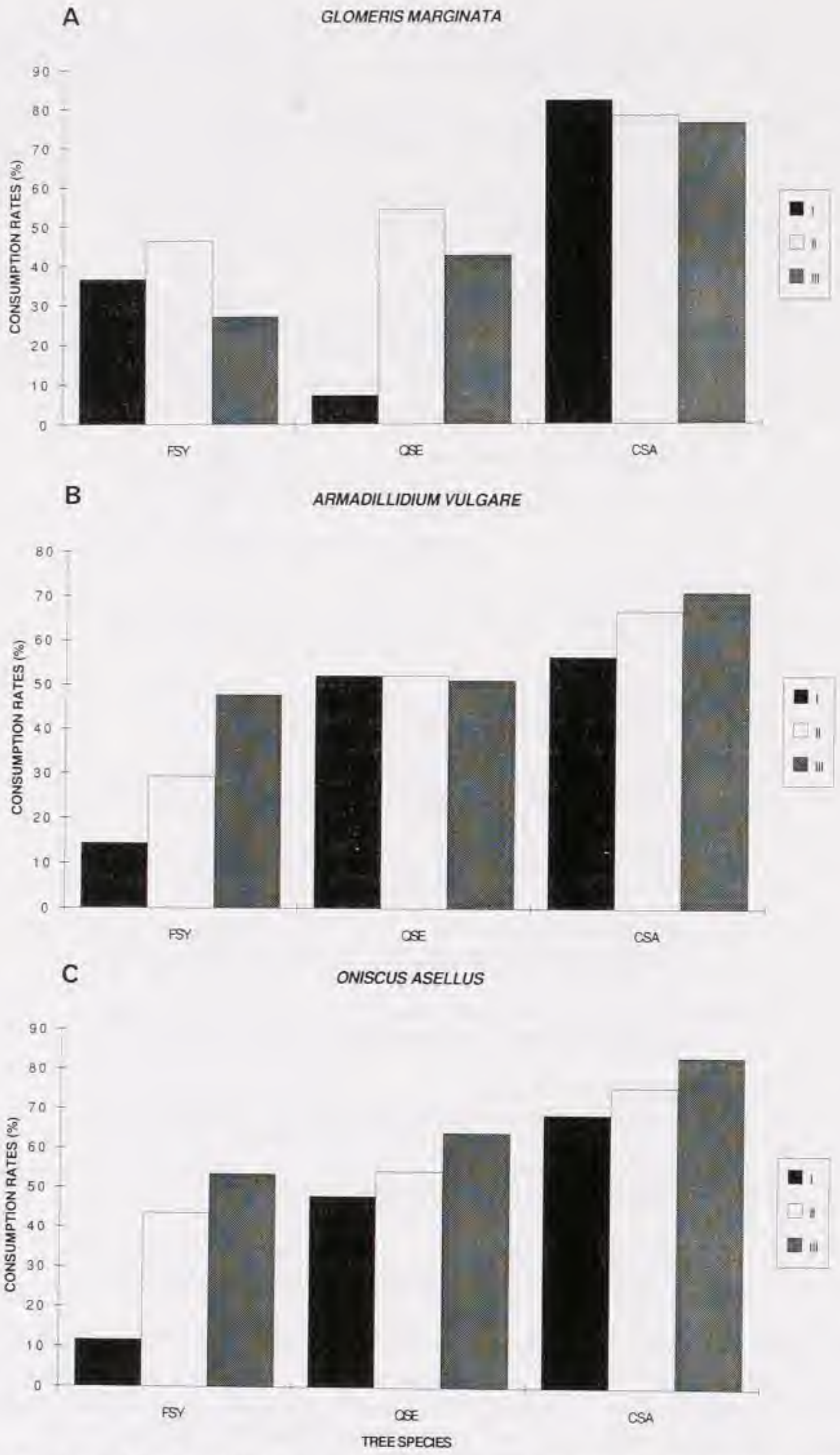


FIG. 1. — Consumption rates (%) of three classes of litter (I, II, III) by one pill-millipede (*G. marginata*) and two woodlice (*A. vulgare* and *O. asellus*) adult individuals fed on *Fagus sylvatica* (FSY), *Quercus sessiliflora* (QSE) and *Castanea sativa* (CSA) leaves.

Source : MNHN, Paris

O. asellus, avoid the thick beech litter of the year. These two species have a similar trophic behaviour against that of *G. marginata* behaviour which is also showed by their preferences to the thin, old beech litter. However, some significant differences were observed between them,*O. asellus* preferring the thick, old beech litter more than *A. vulgare*. Moreover, the three species prefer the chestnut litter to the other types of litter. Though, this was also observed by ANDERSON (1973), it seems no to be directly attribuable to the nitrogen contents, the C/N ratio or even the polyphenol contents of the leaf litter. The same was pointed out by NEUHAUSER & HARTENSTEIN (1978) which indicates however that *Fagus* and *Quercus* litter are "scarcely palatable" to *A. vulgare* and *O. asellus*. Nevertheless, BECK & BRESTOWSKY (1980) say that *O. asellus* grew better on freshly fallen leaves of beech and oak than on overwintered ones which contradicts DUNGER (1958) and PIEARCE (1989) observations. In our essays, they preferred significantly the thick oak litter of the year to the thick beech litter of the year, contrary to *G. marginata*. It seems, however, that the pill millipede is not very common on the beech woods (WALLWORK, 1976), but more common in mixed beech-oak woodlands when oak leaves form part of the litter (VAN DER DRIFT, 1951). In any case, all species preferred old litter to freshly fallen one. The freshly fallen leaves have normally high polyphenol, like lignin, and tannin contents which inhibit their feeding by the animals (MILLER & CAMERON, 1983; RUSHTON & HASSALL, 1983; HASSALL & RUSHTON, 1984; GUNNARSSON, 1987; MOCQUARD *et al.*, 1987; JAMBU *et al.*, 1988).

Besides, it is well known that microorganisms are able to degrade the phenolic and tannin compounds of the leaves, and by that way to render them more palatable to the animals (DUNGER, 1958; HASSALL & RUSHTON, 1984; GUNNARSSON, 1987; BIGNELL, 1989). This can justify the preferences for the old litter, but the preferences for the litter of the year need a more detailed biochemical research.

REFERENCES

ANDERSON, J. M., 1973. — The breakdown and decomposition of sweet chestnut (*Castanea sativa* Mill.) and beech (*Fagus sylvatica* L.) leaf litter in two deciduous woodland soils. II. Changes in carbon, hydrogen, nitrogen and polyphenol content. *Oecologia (Berl.)*, **12** : 275-288.

BECK, L. & BRESTOWSKY, E., 1980. — Auswahl und Verwertung verschiedener Fallaubarten durch *Oniscus asellus* (Isopoda). *Pedobiologia*, **20** : 428-441.

BIGNELL, D. E., 1989. — Relative assimilation of ^{14}C-labelled microbial tissues and ^{14}C-plant fibre ingested with leaf litter by *Glomeris marginata* under experimental conditions. *Soil Biol. Biochem.*, **21** : 819-827.

CANCELA DA FONSECA, J. P. & MEZIANE L., 1978. — Macroarthropodes : abondance relative et activité saisonnière de quelques groupes (Isopodes, Diplopodes, Chilopodes et Opilions). [*In* : LEMÉE G., La hêtraie naturelle de Fontainebleau.] *In :* F. BOURLIÈRE & M. LAMOTTE, *Problèmes d'Écologie : Structure et fonctionnement des écosystèmes terrestres*. Paris, Masson : 116-119.

DUNGER W., 1958. — Über die Zersetzung der Laubstreu durch die Boden-Makrofauna im Auenwald. *Zool. Jb. (Syst.)*, **86** : 139-180.

GEOFFROY, J. J., CÉLÉRIER, M. L., GARAY, I., RHERISSI, S. & BLANDIN, P., 1987. — Approche quantitative des fonctions de transformation de la matière organique par des Macroarthropodes saprophages (Isopodes et Diplopodes) dans un sol forestier à moder. Protocoles expérimentaux et premiers résultats. *Rev. Ecol. Biol. Sol*, **24** : 573-590.

GUNNARSONN, T., 1987. — Selective feeding on a maple leaf by *Oniscus asellus* (Isopoda). *Pedobiologia*, **30** : 161-165.

HARTENSTEIN, R., 1964. — Feeding, digestion, glycogen and the digestive system in *Oniscus asellus*. *J. Insect Physiol.*, **10** : 611-621.

HASSALL, M. & RUSHTON, S. P., 1984. — Feeding behaviour of terrestrial Isopods in relation to plant defenses and microbial activity. *Symp. zool. Soc. London*, **53** : 487-505.

INESON, P. & ANDERSON, J. M., 1985. — Aerobically isolated bacteria associated with the gut and faeces of the litter feeding macroarthropods *Oniscus asellus* and *Glomeris marginata*. *Soil Biol. Biochem.*, **17** : 843-849.

JAMBU, P., JUCHAULT, P. & MOCQUARD, J. P., 1988. — Étude expérimentale de la contribution du crustacé isopode *Oniscus asellus* à la transformation des litières forestières sous chêne sessile. *Pedobiologia*, **32** : 147-156.

MEZIANE, L., 1976. — Activité saisonnière de quelques groupes de Macroarthropodes. Mémoire de DEA d'Écologie animale, Université Paris VI, 54 pp.

Source : MNHN, Paris

MILLER, R. H. & CAMERON, G. N., 1983. — Intraspecific variation of life parameters in the terrestrial Isopod, *Armadillidium vulgare*. *Oecologia (Berl.)*, **57** : 216-226.

MOCQUARD, J. P., JUCHAULT, P., JAMBU, P. & FUSTEC, E., 1987. — Essai d'évaluation du rôle des crustacés oniscoïdes dans la transformation des litières végétales dans une forêt feuillue de l'ouest de la France. *Rev. Ecol. Biol. Sol*, **24** : 311-325.

NEUHAUSER, E. F. & HARTENSTEIN, R., 1978. — Phenolic content and palatability of leaves and wood to soil isopods and diplopods. *Pedobiologia*, **18** : 99-109.

PIEARCE, T. G., 1989. — Acceptability of pteridophyte litters to *Lumbricus terrestris* and *Oniscus asellus*, and implications for the nature of ancient soils. *Pedobiologia*, **33** : 91-100.

RUSHTON, S. P. & HASSALL, M., 1983. — Food and feeding rates of terrestrial isopod, *Armadillidium vulgare* (Latreille). *Oecologia (Berl.)*, **57** : 415-419.

SUTTON, S. L. & HARDING, P. T., 1989. — Interpretation of the distribution of terrestrial Isopods in the British Isles. *Monitor. Zool. ital. (N.S.) Monogr.*, **4** : 43-61.

VAN DER DRIFT, J., 1951. — Analysis of the animal community in a beech forest floor. *Tijdschr. Ent.*, **94** : 1-168.

WALLWORK, J. A., 1976. — *The distribution and diversity of soil fauna*. London, Academic Press, 355 pp.

WARBURG, M. R., 1968. — Behavioural adaptations of terrestrial isopods. *Am. Zool.*, **8** : 545-559.

Source : MNHN, Paris

Ecology and Behaviour of *Xanthodesmus physkon* (Attems, 1898), an Aggregating Paradoxosomatid from Tropical West Africa

Dieter MAHSBERG

Department of Animal Ecology & Tropical Biology (Zoology III), Biocenter
University Würzburg, Am Hubland, D-97074 Würzburg, Germany

ABSTRACT

Xanthodesmus physkon is widely distributed from Central Africa to Liberia. The ecological studies presented here were conducted in the Comoé National Park/Ivory Coast, where a diverse millipede fauna is under research. In addition, experiments on laboratory bred animals are reported. *X. physkon* is restricted to the galery forest and is ecologically separated from the sympatric *Habrodesmus duboscqui)* a soil-dwelling paradoxosomatid occurring in the adjacent savanna. Both species live in aggregations which are formed with the onset of the newborns' surface activity; adults live solitarily. Aggregations of *X. physkon* comprise 150 to 700 individuals; after fusion, they may consist of 10,000 specimens. Disturbing or hurting of only one individual instantly leads to a dissolving of aggregations for a certain time and corroborates the anti-predatory function of this behaviour. The millipedes avoid spots where a conspecific was disturbed. Escape and avoiding behaviour are elicited by secretions of the defensive glands. The large number of *X. physkon*-sclerites in the food middens of *Paltothyreus tarsatus* points to this abundant stink ant as a possible predator of these millipedes but attacks were rarely observed in the field. In the laboratory, stink ants mostly avoid contact with live *X. physkon. X. physkon* are mainly found on the bark of trees where they exclusively feed on algae. Tree species with a high density of algae are prefered. The activity of *X. physkon* is restricted to the the most humid periods of the rainy season (April to August). Aggregations in the laboratory in Germany which were permanently kept under favourable conditions (high soil humidity, 27°C, D:L = 12:12), showed an extraordinary activity pattern: surface activity and moulting cycles among individuals were highly synchronized, with distinct peaks of activity in the intermoult phases. One period of total inactivity of six months occurred. The activity patterns of separately kept aggregations were nearly coincident, with a deviation of only a few days. This is a hint at an endogenous rhythm in the activity of *X. physkon* which adjusts it to the seasonal climate of its tropical habitat.

RÉSUMÉ

Écologie et comportement d'un Paradoxosomatidae grégaire d'Afrique tropicale occidentale : *Xanthodesmus physkon* (Attems, 1898).

X. physkon s'étend de l'Afrique centrale au Libéria. Des recherches écologiques ont été menées dans le Parc National de la Comoé (Côte d'Ivoire) où la faune de Diplopodes est très diversifiée, ainsi qu'en laboratoire. *X. physkon* se cantonne dans la forêt-galerie et se distingue écologiquement d'*Habrodesmus duboscqui*, un Paradoxosomatidae édaphique sympatrique qui se rencontre dans la savane adjacente. Les deux espèces présentent un mode de distribution agrégatif dont les amas se constituent lors du début d'activité de surface de la nouvelle génération, les adultes vivant en solitaire. *X. physkon* s'agrège en amas composés de 150 à 700 individus; après fusion, les agrégats peuvent réunir 10000

MAHSBERG, D., 1996. — Ecology and behaviour of *Xanthodesmus physkon* (Attems, 1898), an aggregating paradoxosomatid from tropical West Africa. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 585-586. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

spécimens. Le fait de perturber ou de blesser un seul d'entre eux provoque une dissolution des agrégats et vient corroborer la fonction antiprédation de ce comportement. D'ailleurs, ces Diplopodes évitent les endroits où un groupe conspécifique a été perturbé. De tels comportements de fuite ou d'évitement sont provoqués par les sécrétions émises par les glandes défensives. Une grande quantité de sclérites de *X. physkon* rencontrés dans les résidus alimentaires de la fourmi-cadavre *Paltothyreus tarsatus* montre que cette fourmi peut éventuellement jouer un rôle de prédateur sur les populations de Diplopodes. Toutefois, les attaques directes sont très rarement observées sur le terrain. Au laboratoire, ces fourmis évitent la plupart du temps tout contact avec les individus vivants de *X. physkon*. Ces derniers se rencontrent principalement sous les écorces, où il se nourrissent exclusivement d'algues. On note une préférence marquée pour les essences qui accueillent une forte densité d'algues. L'activité de *X. physkon* est limitée aux périodes les plus humides de la saison des pluies (avril à août). Les agrégations obtenues en laboratoire en Allemagne ont été maintenues en permanence dans des conditions favorables (humidité du sol élevée, 27°C , D:L = 12:12). Elles montrent des modalités d'activité extraordinaires : l'activité de surface et les cycles de mue entre les individus sont hautement synchronisés, présentant des pics d'activité distincts au cours des phases d'intermue. Une période d'inactivité totale s'étend sur six mois. L'activité d'agrégats élevés séparément est en coïncidence presque totale, avec une marge de différence de quelques jours seulement. Ceci amène à penser que le rythme endogène de l'activité de *X. physkon* s'ajuste bien aux phases climatiques saisonnières de son environnement tropical.

Source : MNHN, Paris

Déplacements en masse dans le sud-est de la France chez *Ommatoiulus sabulosus* (Myriapoda, Diplopoda, Julidae) avec invasions d'habitations

François **SAHLI**

Muséum National d'Histoire Naturelle, Zoologie/Arthropodes, 61, rue de Buffon, F-75231 Paris Cedex 05
& Laboratoire Souterrain du C.N.R.S., F-09200 Moulis, France

RÉSUMÉ

Deux cas sont décrits et analysés : l'un concerne la Provence en 1987, l'autre les Alpes-Maritimes en 1988. Ces cas, personnellement observés *in situ*, ont trait à *Ommatoiulus sabulosus*. L'auteur cherche à répondre à diverses questions et à interpréter le phénomène des rassemblements et des migrations en masse, en tenant compte des connaissances actuelles sur la périodomorphose.

ABSTRACT

On mass migrations with dwelling invasions in Mediterranean *Ommatoiulus sabulosus* (L.) (Myriapoda, Diplopoda, Julidae) in the south-east of France.

The two mass migrations (MM) observed at the Val de Sibourg (Provence) and at Peillon (Alpes-Maritimes) are the result of a double overpopulation - viz. in spring and in a same place - (a) of countless "tall individuals" (most of them being post-adults), with, in addition, (b) countless very young larvae, which originated from egg depositions during the previous autumn. The presence of shelter sites (or relay shelters) seems to have play a role in Peillon. In South of France, mass migrations with dwelling invasions can only occur if a village or a part of it (often a recent construction) is set up in the garrigue or more or less near a large garrigue. The year of the mass migration, spring rains are a *sine qua non* condition. In addition to spring rains of the year y, heavy rains during the previous autumn seem to have play an important role in the case of Peillon. Finally, the influence of predators and parasites on (a) the population which got adult in 1984 and on (b) the individuals born in 1984 (which gave adults in 1986 or 1987) seems to have been poor. Such situations - combined with the adoption of "explosive" juvenile to adult maturation moult strategies several times (instead of spreading "CAT" strategies) - allowed a first demographic explosion in 1984, followed by other explosions in 1986, 1987 at Sibourg and 1987, 1988 at Peillon.

INTRODUCTION

Les déplacements en masse de diplopodes sont connus depuis la fin du siècle dernier. Ils présentent deux cas extrêmes : (1) ceux effectués par un très grand nombre d'individus (jusqu'à des centaines de milliers), (2) les déplacements ne comportant qu'un petit nombre d'individus. Les premiers seront appelés "migrations en masse" (MM). Les seconds, appelés migrations ou déplacements tout court, seront désignés par M. Dans les cas extrêmes, la limite entre les deux types est nette. Il existe néanmoins des cas où la séparation est floue et devient affaire

SAHLI, F., 1996. — Déplacements en masse dans le sud-est de la France chez *Ommatoiulus sabulosus* (Myriapoda, Diplopoda, Julidae) avec invasions d'habitations. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 587-598. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

d'appréciation subjective. Parmi les MM, on distingue celles comportant l'invasion d'habitations humaines et celles ne la comportant pas.

Chez *O. sabulosus* , on se doit de mentionner tout d'abord une migration en masse en Alsace (France) en 1900 (VERHOEFF, 1900). Des milliers de *O. sabulosus* se sont déplacés sur une voie ferrée et sont parvenus à bloquer un train dont les roues patinèrent. Dans les années 1950, un déplacement de *O. sabulosus* a été observé dans la région de Cologne en Allemagne (SEIFERT, *comm. pers.*). En 1973, un autre déplacement important eut lieu en Sarre (Allemagne) (HELB, 1975) et a fait la une des journaux : les sarrois du village d'Ensdorf (non loin de Sarrelouis) - particulièrement ceux du *nouveau lotissement* de l'époque - furent paraît-il épouvantés de trouver des iules dans leurs assiettes, sur leurs tables de cuisine ou dans leurs lits, ce qui nous semble avoir été exagéré par la presse. En Provence (France), le seul cas signalé est celui mentionné par DEMANGE (1960, 1963) dans les Alpes-de-Haute-Provence.

Il faut insister sur le fait que toutes les invasions de *O. sabulosus* qui se sont produites en France et en Allemagne dans le passé n'ont jamais été observées directement par les auteurs qui en ont parlé dans leurs publications ; de plus, la biologie *s. l.* et les cycles des *O. sabulosus* étaient alors presqu'inconnus (cf. SAHLI 1990a, 1991a). Les observations elles-mêmes, sur le terrain, ont été faites par des témoins n'ayant pas forcément la rigueur et la compétence scientifiques voulues, qui ont assisté au phénomène ou qui en ont "souffert" ; d'où des possibilités d'imprécisions, de déformations et d'exagérations des faits. (Dans un journal allemand , en guise de *O. sabulosus*, un Spirobolide a été représenté en photographie !).

Des déplacements d'*O. sabulosus* ont été signalés par HALKKA (1958) en Finlande et par FAIRHURST (1968, 1969) en Grande-Bretagne : peut-être ne s'agit-il dans les deux cas que de M et non de MM (?). Quoi qu'il en soit, il semble qu'il ne s'agisse pas du phénomène que nous traitons ici. Des MM de *Ommatoiulus moreleti* , avec invasions d'habitations, ont été signalées dans le cas particulier de populations introduites par l'homme en Australie (BAKER, 1978a, b, c, 1979, 1984), cas qui ne sera pas analysé ici.

Nous avons personnellement assisté, sur le terrain, à 3 MM : une en Yougoslavie en 1969 (SAHLI, 1984) concernant *Pachyiulus fuscipes*, une au Val de Sibourg près de Lançon-de-Provence (France) en 1987 et une à Peillon dans le Mentonnais (Alpes-Maritimes, France) en 1988. Nous n'envisagerons que les deux derniers cas qui concernent *O. sabulosus*.

MATÉRIEL

Les animaux étudiés sont des *Ommatoiulus sabulosus aimatopodus* (*in* DEMANGE, 1981), *sabulosus punctatus* et *apunctulatus* selon VERHOEFF (1921 a, b). L'ornementation et la coloration du tégument permettent de distinguer deux "races" géographiques, réparties dans deux zones situées de part et d'autre du Var. En outre, les animaux localisés à l'Ouest du Var (zone : Cannes, Grasse, Antibes, Bouches-du-Rhône) sont nettement plus sveltes que ceux habitant à l'Est du Var (zone : arrière-pays niçois et Mentonnais). D'autres types d'ornementation et de coloration différents des précédents existent dans 2 autres zones, d'une part près de Toulon (Var), d'autre part dans les Alpes-de-Haute-Provence (Colmars).

EXPOSÉ SOMMAIRE DES CAS

Le cas du Val de Sibourg

La MM étudiée a eu lieu à la mi-avril 1987 (essentiellement les 16, 17, 18 avril). Nos investigations ont été effectuées, *in situ,* au lotissement du Val de Sibourg, commune de Lançon, à quelques kilomètres de Salon-de-Provence (Bouches-du-Rhône). Lançon lui même est resté indemne tandis que dans le Val de Sibourg seul un quartier a été fortement touché. La majeure partie du lotissement, constitué de maisons individuelles, était de construction récente (1-3 ans) tandis qu'une partie était encore en construction au moment des faits. D'autres invasions ont été signalées dans des villages voisins (Ventabren, La Barben) aux mêmes dates.

Les iules sont descendus des collines environnantes occupées par de la garrigue. Le "Camp long" a constitué l'arrivée majeure Est. Les populations de *O. sabulosus* de cette colline sont pratiquement encerclés par un ensemble de canaux (canal du Verdon, canal EDF, canal de

Source : MNHN, Paris

Marseille) et par la ville d'Aix-en-Provence. Face au lotissement du Val de Sibourg, qui a été envahi, existe une issue terrestre Est et Nord-Est constituée par un pont. Une bonne partie des animaux en migration ont emprunté ce pont ainsi que la partie de la colline où le canal est souterrain. D'autres ne l'ont pas franchi : ils ont été arrêtés par la partie aérienne du canal (constituant une barrière) et sont restés suspendus aux parois externes et internes du canal. A plus grande échelle (chaîne de la Trévaresse, chaîne des Côtes, chaîne d'Eguilles, etc.) les iules sont en fait encerclés entre la Durance, le Canal de Marseille, l'Arc et la ville d'Aix-en-Provence.

Des milliers d'iules, provenant de la garrigue environnante (qui recouvrait le lotissement avant sa construction), se sont déplacés dans les rues, sur les trottoirs, les murs de clôture et les murs extérieurs des maisons (parfois, pour un petit nombre d'individus, sur les murs intérieurs de certaines habitations).

Le déplacement est survenu après les fortes pluies de la première moitié d'avril.

Quatre générations participent au déplacement : trois générations de 1983, 1984 et 1985, [les individus nés en automne 1984 (âgés d'un an 1/2) étant majoritaires par rapport aux autres] ; une génération de petites larves à 4 ou 5 rangées d'ocelles (RO) de l'année 1986 (larves issues des pontes de l'automne 1986), elles aussi, particulièrement nombreuses. Après l'intervention des pompiers à l'aide de gaz toxiques, un amoncellement de jeunes larves, mortes ou à demi-mortes, pouvaient s'observer dans les caniveaux sur une épaisseur de 10 à 15 cm. De nombreux individus de toute taille accrochés aux murs du canal furent épargnés par l'intervention des pompiers qui craignirent de contaminer l'eau. Au cours de cette "invasion" de printemps 1987, il convient de noter la participation de jeunes larves nées l'automne précédent (âgées de 6 à 7 mois) : des larves aussi jeunes ne figuraient dans les MM précédemment analysées, ni chez *O. sabulosus* (au printemps, en Alsace et en Allemagne), ni chez *P. fuscipes* (en automne en ex-Yougoslavie).

Le cas de Peillon

L'invasion a commencé début avril 1988, un an environ après celle de Sibourg. Deux parties du village de Peillon ont été envahies. On distingue d'une part, un foyer principal N.N.W, concernant quelques maisons de construction plus ou moins récente localisées sur la D121 à l'entrée du village, le cimetière, la chapelle des Pénitents blancs ; d'autre part un foyer Est situé à l'extrémité supérieure du village englobant l'église et quelques maisons individuelles (de construction ancienne) proches. Les deux foyers sont disjoints.

Caractéristiques sommaires :

Le déplacement eut lieu après de fortes pluies. La partie Nord et Nord-Ouest du foyer principal, boisée (essentiellement d'oliviers), comporte une couverture végétale protégeant mieux des pluies torrentielles que la garrigue peu dense des versants alentour. Le foyer de l'église, quant à lui, est bordé par un à-pic rocheux, inaccessible à l'Homme, recouvert d'une garrigue dense d'où proviennent les animaux.

Aux alentours des foyers, sur les hauteurs de la zone N et NW ainsi que sur les collines environnantes, il n'y a que fort peu d'individus (les animaux ayant probablement quitté ces collines pour se concentrer dans le foyer Nord-Ouest).

Trois générations sont présentes sur les sites d'invasions : deux des années 1984 et 1985, (avec une prédominance des individus nés en 1984) et une constituée de petites larves (4-5RO) issues des pontes de l'automne 1987.

Les grands individus (larves âgées, adultes, post-adultes des générations 1984 et 1985) migrent, en un premier temps, en avril. Les petites larves de 1987 - alors qu'elles appartiennent maintenant aux stades 5 et 6RO - apparaissent en grand nombre dans un second temps, en mai, sur les murs des maisons, de l'église, de la chapelle et sur les tombes en marbre du cimetière (donc dans les deux zones d'invasion). Contrairement au Val de Sibourg (où le développement est plus rapide), il y a ici décalage dans le temps entre les déplacements sur les murs, d'une part,

Source : MNHN, Paris

des générations 1984 et 1985 et d'autre part de la génération de 1987 (son développement est en retard de 1 à 2 mois sur celui de Sibourg).

INTERPRÉTATIONS ET DISCUSSION

A un endroit donné, on constate une concentration massive d'individus dont la mobilité est incontestablement en rapport avec de fortes pluies. Tentons de répondre aux principales questions qui se posent.

Origines de la concentration

a) On peut envisager une origine géographique soit proche (déplacements courts de l'ordre de plusieurs mètres à plusieurs centaines de mètres), soit lointaine (5 à 10 km ou plus?).

En ce qui concerne le Val de Sibourg et ses environs, rien n'empêche de penser qu'il y a eu déplacement par rayonnement, à partir de la vaste garrigue, par l'ensemble (ou une partie) des points de sortie possibles (ponts, passages aériens correspondant aux passages souterrains des canaux). Le Val de Sibourg représenterait l'un de ces points d'échappement. Ce rayonnement a pu s'effectuer, soit à partir du petit encerclement constitué par les canaux, soit à partir du grand encerclement faisant intervenir la Durance.

En ce qui concerne Peillon, nous pensons que les animaux ayant migré en avril 1988 étaient déjà sur place en hiver 1987-88 et/ou au printemps 1988. L'expérience acquise montre bien que, dans les Alpes-Maritimes, les pluies torrentielles automnales et printanières entraînent un abandon des sites, notamment à euphorbes, à romarin et à lavande, par les populations de *O. sabulosus*. Il est probable que les individus concentrés au printemps 88, proviennent (au moins *pro parte*) de déplacements effectués en automne 1987 lors des accouplements et surtout suite aux fortes pluies du 5 et 10 octobre 1987. Le même raisonnement peut s'appliquer aux *O. sabulosus* de la région de Sibourg. La migration aurait ainsi pu s'effectuer en plusieurs temps.

b) La concentration n'a pas uniquement une origine géographique. On note, aussi bien au Val de Sibourg qu'à Peillon, une prédominance des individus nés en automne 1984, année tout à fait exceptionnelle par le nombre des pontes (abondance des femelles pondeuses et étendue des sites de ponte) non seulement dans le sud-est de la France, mais aussi, paradoxalement, en Bourgogne (Côte d'Or, Porron) et en Allemagne (Sarre) (SAHLI, inédit).

Le développement post-embryonnaire se déroulant avec peu de pertes, comme ce fut le cas cette année de pontes abondantes (APA), il est suivi, deux ans plus tard à Sibourg et 3 ans plus tard à Peillon, d'une année d'abondance amplifiée des femelles adultes (AAA = année d'abondance des adultes, femelles ou mâles) et des pontes (APA) ; ce qui s'est effectivement passé.

Déplacements et activité

Outre la concentration et la surpopulation, les déplacements sont liés à l'activité de l'espèce, dont on distingue 7 types en Provence et Côte d'Azur : (a) une activité post-exuviale, (b) une activité déclenchée par des fortes pluies ou (c) par un temps lourd orageux (SAHLI, 1986c), (d) une activité sexuelle au moment de l'accouplement, (e) une activité propre aux femelles fécondées cherchant un lieu de ponte, (f) une activité nocturne (FAIRHURST, 1968), (g) une activité des femelles (en mai-juin) liée à la nutrition.

Dans la journée, à certaines périodes de l'année (par exemple en mai) les iules peuvent ne pas utiliser leurs abris diurnes et demeurer inactifs soit à l'air libre, comme en altitude (Rocca Spaviera, Peïra Cava : prairie avec herbe de 3 à 5 mm de haut, broutée par les moutons, comportant à proximité des buissons de buis, de *Juniperus*, des touffes d'euphorbes et de lavande), soit abrités (Rocca Spaviera, Peïra Cava, ruines de Chateauneuf-de-Contes, Peillon, Baousset, etc).

Source : MNHN, Paris

Les déplacements de Sibourg et de Peillon sont en rapport avec les causes d'activité (a) et (b) : les individus sortaient de leur mue hivernale et il y a eu de fortes pluies coïncidant avec la l'activité post-exuviale. A ces deux facteurs s'ajoute une surpopulation. Les déplacements à distance eurent éventuellement lieu de nuit (type f) en plusieurs étapes. Des expériences inédites et les observations faites sur une dizaine d'années dans les Alpes-Maritimes démontrent l'influence des précipitations violentes et soudaines avec un risque réel de noyade (cas observés au Pas de l'Escous), les ouvertures métamériques des trachées étant localisées face ventrale, ainsi qu'une réaction de fuite (SAHLI, 1984).

Le décalage dans le temps entre les invasions de Provence (1987) et celles du Mentonnais (1988)

Ce décalage s'explique par une différence dans le rythme des pontes abondantes. Compte tenu des circonstances environnementales, les pontes exceptionnellement abondantes de 1984 ont conduit 2 ans plus tard à Sibourg, 3 à Peillon, à une abondance d'adultes. On note des différences dans le temps des mues de maturations juvéniles-adultes (= MMJ), variables selon les sites et les années (SAHLI, 1992). Dans d'autres circonstances, les individus nés en 1984 à Sibourg auraient, très bien pu pondre massivement 3 ans après leur naissance, au lieu de 2. De même, les individus de 1984 de Peillon auraient pu pondre 2 ans ou 4 ans après, au lieu de 3. En outre, au lieu de massives ou explosives, les pontes auraient pu être plus ou moins équitablement étalées sur 2, 3 et éventuellement 4 années (stratégie CAT , SAHLI, 1990a, b, 1991a, b).

La double surpopulation

L'analyse des MM de Sibourg et de Peillon se rapporte à trois points.

a) Concentration dans un même endroit et au printemps des adultes, post-adultes, intercalaires et des larves âgées, appartenant à 2 ou 3 générations. Celle de 1984 est la plus nombreuse, elle correspond aux descendants d'une année de pontes abondantes. La surpopulation des femelles est en fait due à celles ayant pondu l'automne précédent, celle des mâles est due aux intercalaires (cas de Sibourg). La surpopulation est donc essentiellement le fait d'animaux post-imaginaux. Elle peut se schématiser ainsi, IN représentant les adultes, post-adultes, intercalaires et larves âgées : IN1983 + IN1984 (APA) + IN1985 = surpopulation d'IN (SIN) au printemps dans un même site (1987 à Sibourg, 1988 à Peillon où les IN1983 font défaut).

b) Concentration de pontes puis de jeunes larves de 2 (voire 3) générations dans un même endroit et la même année. La majorité de ces pontes est le fait de mâles ad1 ou/et ad2 surabondants, provenant eux-mêmes d'une APA (génération de 1984). Ces pontes automnales de l'année x conduisent au printemps suivant (x+1) à une surpopulation de jeunes larves (SJL).

Dans le cas de Sibourg, (P = ponte d'une année) les choses se passèrent probablement ainsi : "P1986 (des IN1983) + P1986 (des IN1984, APA de 1984) + ?P1986 (des IN1985) = APA1986".

Tout porte à croire qu'il y a eu prédominance des P1986 (des IN1984). Il y a eu répétition dans le temps de deux APA, l'une en 1984, l'autre en 1986 (Sibourg). Dans les 2 MM observées, les pontes ont été explosives deux fois de suite : en 1984 (APA à Sibourg et Peillon) et en 1986 (APA à Sibourg) ou en 1987 (APA à Peillon).

L'expérience montre que d'autres situations sont possibles lorsqu'il n'y a pas de MM. D'une part, les sites de ponte de 2 générations peuvent être différents dans l'espace (changement de sites de ponte) ; d'autre part, les pontes d'une même génération peuvent être réparties équitablement ou non dans le temps sur plusieurs années : stratégie de répartition "CAT" (SAHLI, 1991 b) , l'opposé d'une stratégie explosive.

c) Réunion dans un même endroit et la même année d'une surabondance d'adultes, post-adultes, intercalaires et larves âgées (SIN), encore en vie dans le site, avec une surabondance de jeunes larves (SJL). Avant la MM dans les aires d'origine on a une double surpopulation SIN+SJL (à Sibourg, elle s'observe simultanément dans les aires post-migratoires tandis qu'à

Source : MNHN, Paris

Peillon il y a un léger décalage dans le temps). Après avoir pondu, les femelles adultes quittent souvent le lieu de ponte (Col de Braus), alors que dans le cas des MM de Sibourg et de Peillon, mâles et femelles post-imaginaux se trouvent dans le même endroit que les pontes et les larves qui en sont issues. A Sibourg, tant qu'il n'y a que des oeufs (automne 86), puis des larves à 2-3(4)RO (automne 86, hiver 86-87), la densité dans les aires d'origine correspond simplement à une seule surpopulation. Lorsqu'au printemps 87, après l'hivernation, les larves parvenues aux stades 4-5RO se mettent à se déplacer et à manger abondamment, il y a une double surpopulation, traduite par une densité accrue, dont les effets se font sentir sur l'ensemble de la population. Notons que les points b et c ne s'appliquent pas à la migration en masse automnale de *P. fuscipes* en Yougoslavie.

A Sibourg, selon le point a, la ponte abondante de 1986 s'explique par la présence de nombreux adultes cette année-là (AAA1986), provenant pour la plupart de la génération exceptionnellement abondante de 1984. Mais, pour qu'il y ait beaucoup de femelles post-adultes et d'intercalaires mâles au printemps 1987, il faut nécessairement un maintien en vie qui conduit les mâles et les femelles de la génération 1984, devenus ad1 en 1986, à des individus post-imaginaux en 1987.

Le maintien en vie, l'année suivante, des femelles et des mâles après l'accouplement et la ponte

a) Chez les femelles, il s'explique soit par l'existence d'une itéroparité directe ou indirecte (SAHLI, 1993) chez les femelles, les femelles ad1 ayant pondu en 1986 resteraient capables de se reproduire une nouvelle fois en 1987 (itéroparité directe), en 1988 ou en 1989 (itéroparité indirecte) ; soit, plus vraisemblablement, par la possibilité d'un maintien en vie des femelles ad1 de 6 mois à 10-12 mois après la ponte, comme celà s'est produit dans les élevages. Dans cette hypothèse, la survie passagère serait suivie de mort, sans qu'il y ait eu itéroparité, pouvant représenter un vestige d'une stratégie ancestrale (caractère génétique ancestral d'itéroparité femelle). Cet hypothétique caractère ne s'exprimerait plus (ou peu ou rarement?) dans les conditions de température et de pluviosité qui règnent, à faible altitude, dans le sud-est de la France. L'itéroparité a d'autant moins de raisons de s'exprimer dans ces sites que le nombre d'oeufs produits (et pondus en une fois) par femelle est important (de l'ordre de 500). Le caractère ancestral pourrait aussi ne pas pouvoir s'exprimer dans le cas d'une forte surpopulation comme c'est le cas ici. L'itéroparité chez *Ommatoiulus* pourrait traduire une adaptation au froid de l'époque glaciaire (SAHLI, 1990a, b : glacier du Mercantour il y a 20000 ans). Les choses purent se passer ainsi : production et ponte d'un nombre relativement petit d'oeufs (très inférieur à l'actuel) avec répétition des pontes à des intervalles de plusieurs années et des périodes de repos entre 2 pontes comme celà a été admis chez les femelles de *Typhloblaniulus* (SAHLI, 1993). L'itéroparité ancestrale présumée des femelle de *O. sabulosus* serait sous la dépendance d'un ou de plusieurs gènes non liés au sexe et aurait pu se manifester autrefois aussi bien chez les femelles que chez les mâles. Notons que le comportement de *O. sabulosus* (notamment des femelles), après la migration, donne l'impression d'un "suicide" collectif : inactivité, exposition aux conditions environnementales, déshydratation et mort alors qu'ils pourraient se protéger et se nourrir dans la garrigue toute proche.

b) Chez les mâles, le mécanisme de survie est la périodomorphose, phénomène à détermination génétique probable (SAHLI, *passim*), propre à certains diplopodes et conduisant à des mâles post-imaginaux. Les espèces à mâles périodomorphiques ou à mâles post-imaginaux itéropares sans régression (succession adulte-adulte = stratégie γ) sont des espèces anciennes, ayant probablement déjà vécu à l'époque glaciaire. Les espèces à mâles périodomorphiques présentent un grand avantage : elles sont, grâce à la périodomorphose et aux intercalaires de longue durée, [formes beaucoup plus résistantes à un environnement défavorable que les mâles adultes (SAHLI, 1991c)] et peut-être grâce à l'itéroparité indirecte des femelles, adaptées aux changements de climat, sans être obligées d'avoir recours à une spéciation, aussi bien dans un

Source : MNHN, Paris

sens (froid, période glaciaire) que dans l'autre (périodes interglaciaires). Cette adaptation permet aussi une grande extension géographique actuelle Nord - Sud, des plaines basses aux sommets montagneux de 3000 m. d'altitude, avec possibilité d'occuper divers écosystèmes (forêts, prairies, garrigues, etc.). D'après nos recherches expérimentales, les intercalaires de *O. sabulosus* paraissent mieux adaptés (plus résistants) au froid qu'à la chaleur (SAHLI, 1991c).

A Sibourg, le schéma du développement mâle retenu est le suivant : ad1 (automne 1986, nés en 1984) - intercalaires (printemps 1987, mâles dédifférenciés retrouvant une morphologie quasi-juvénile) - ad2 (été-automne 1987 après une mue de maturation). Les mâles intercalaires sont extrêmement nombreux au printemps 1987, le rapport intercalaires / tous les autres mâles (juvéniles de 7 à 1ORO + ad1) est de 3/1 (SAHLI, 1990), le rapport intercalaires/femelles (individus de 9 à 13RO) est de 1/1,55. Ceci confirme clairement trois règles - (r1) : dans de bonnes conditions, presque tous les mâles ad1 peuvent se transformer en intercalaires (SAHLI, 1986 b) ; (r2) : les intercalaires s1 sont nombreux une année x lorsque les adultes ad1 dont ils sont issus étaient eux-mêmes nombreux l'année x-1 (SAHLI 1986a). Le cas de Sibourg démontre bien qu'après de bonnes mues de maturations des juvéniles en ad1 (MMJ) et lorsque tous (ou presque tous) les individus sont rassemblés en un point suite à une MM (au lieu d'être dispersés d'une façon irrégulière) la fréquence des intercalaires s1 peut être très élevée ; (r3) : à faible altitude, en Provence et dans les Alpes Maritimes, la grande majorité des mâles ad2 meurent à l'automne de l'année x (SAHLI, inédit), d'où la rareté des s2.

A Peillon, en automne 1986 (sécheresse), les mâles ad1 (nés en APA-1984) sont nombreux, bien qu'il demeure une fraction de mâles juvéniles tardifs non transformés en ad1 en 1986. Les femelles sont vraisemblablement restées majoritairement juvéniles en 1986.

L'affirmation selon laquelle il n'y eut probablement que très peu de pontes en 1986 à Peillon repose sur les raisons suivantes : des larves 4-5RO au printemps 1987, des larves 7-8-9RO au printemps 1988 et des individus 9-10RO au printemps 1989 étaient peu nombreux, voire rares ; or, ils auraient été nombreux (au moins par moments) s'il y avait eu des pontes abondantes en automne 1986 et ils n'auraient pu échapper à l'observation pendant plusieurs années, sauf en cas d'émigration massive sans retour ; de plus, ce que nous venons de dire de Peillon au sujet de la rareté des pontes en 1986 est valable pour d'autres stations du Mentonnais.

Au printemps 1987 et à Peillon, les intercalaires s1 devaient, en principe, être nombreux à certains endroits. En automne 1987 (pluies torrentielles dépeuplant les sites d'observation par émigration) les ad2 (issus des s1) devaient, en principe, être nombreux eux aussi à certains endroits. Or, dans les endroits prospectés et là où des animaux ont pu être trouvés, les s1 du printemps 1987 et les ad2 de l'automne 1987 étaient peu nombreux. Nous ignorions qu'une MM allait se produire en 1988 à l'entrée du village et au cimetière ; l'entrée du village n'a donc pas été prospectée au printemps et à l'automne 1987. Nous n'avons pas non plus pu trouver d'animaux en automne 1987 aux environs de l'église (balayages trop fréquents). La plupart des femelles ad1 nées en 1984 sont devenues matures en 1987 (comme dans d'autres sites du Mentonnais). Ce sont en majeure partie les mères des nombreuses larves nées en 1987. A l'automne 1987, la situation s'interprète ainsi : (cr1) croisements majoritaires ad2 mâles nés en 1984 x ad1 femelles nées majoritairement en 1984, donc décalage d'un an entre les premières maturations mâles et femelles ; (cr2) croisements minoritaires ad1 mâles tardifs nés en 1984 x ad1 femelles de 1984 ; (cr3) croisements minoritaires de quelques ad1 mâles nés en 1985 x ad1 femelles de 1984 et éventuellement de 1985. Des ad2 mâles d'automne 1987 de Peillon, seul un tout petit nombre a survécu (r3) et s'est transformé, au printemps 1988, en intercalaires s2 qui, vu leur très faible nombre, n'ont peut-être pas figuré dans les prélèvements des animaux en migration au printemps 1988. Le résultat est que lors de la migration de Peillon, contrairement à celle de Sibourg, les intercalaires étaient relativement peu nombreux (le rapport intercalaires/femelles varie entre 1/1,7 et 1/2 selon les endroits).

Concernant les *O. sabulosus* méditerranéens de faible altitude, il en résulte une quatrième règle (r4) corollaire de la troisième : les mâles adultes peuvent être nombreux un automne x et les intercalaires peu nombreux au printemps x+1 lorsque les adultes en question étaient des ad2. Une ponte abondante à l'automne x, suivie d'abondantes larves au printemps x+1, peut masquer

Source : MNHN, Paris

les géniteurs mâles adultes réels de l'automne x lorsque ceux-ci sont des ad2. Dans ce cas, les intercalaires peu nombreux récoltés au printemps x+1 sont pour la plupart des s1 et ne dérivent par conséquent pratiquement pas des géniteurs ad2, morts en majorité. A Sibourg, au printemps 1987, il s'agissait, *grosso modo*, d'intercalaires 1 âgés de 2 ans et demi. A Peillon, au printemps 1988, la plupart des ad2 étant morts, il n'y avait que quelques intercalaires s1 de la génération 1985 (âgés de 2 ans et demi), plus quelques rares intercalaires pouvant être des s1 tardifs, âgés de 3 ans et demi et correspondant peut-être aux juvéniles tardifs de 1986.

Le faible nombre des intercalaires s1

Le nombre des intercalaires peut être également plus ou moins faible dans le cas où il n'y a pas explosion d'adultes, c'est-à-dire lorsque la production des adultes n'est plus explosive et concentrée sur une année comme en 1986 à Sibourg mais répartie plus ou moins équitablement sur deux à quatre ans. Dans ce cas, le nombre des larves d'une génération susceptibles de devenir adultes est fractionné : certaines restent juvéniles, d'autres deviennent adultes ad1. Nous pouvons admettre les rapports 50/50 ou 40/60 sur deux ans, 10/55/35 ou 10/40/40 sur 3 ans, etc. La règle (r4), corollaire de la règle (r1) intervient alors : lorsque les adultes ad1 sont produits en petite quantité, parce que leur production est plus ou moins largement fractionnée une année x, les intercalaires 1 de l'année x+1 sont peu nombreux et leur nombre dépend de l'importance de la fraction d'ad1 de l'année x.

Une faible quantité d'intercalaires une année donnée dans un site donné peut donc avoir au moins deux raisons : (rai1) l'existence de géniteurs ad2 ou (rai2) l'adoption d'une stratégie de fractionnement CAT. Il y a une troisième raison (rai3) : l'existence d'une distribution non homogène d'intercalaires (SAHLI, 1991a) qui fait que le nombre d'intercalaires récoltés à un endroit donné ne traduit pas leur effectif réel dans la population. Il existe enfin une quatrième raison (rai 4) : la délocalisation d'un site (par exemple du site de naissance) par émigration de la quasi-totalité de la population dans un autre, suite à des pluies torrentielles de printemps ou/et d'automne et sans qu'il y ait pour autant invasion d'habitations, ces dernières faisant défaut.

Compte tenu des raisons 3 et 4, une MM présente l'avantage de rassembler tous les individus (ou une bonne partie d'entre eux), intercalaires compris, au point de migration. Il en résulte une cinquième règle (r5) : il est nécessaire de bien connaître un site donné et les antécédents biologiques des animaux qui y vivent (pontes, jeunes larves, apparition des stades plus âgés au cours des printemps et automnes successifs, maturation sexuelle des mâles (ad1), apparition d'intercalaires). Même cela n'est pas suffisant puisque nous venons de voir qu'il peut y avoir des évacuations massives dues aux antécédents environnementaux. Le nombre faible d'intercalaires observé une année x dans un site, lorsque les antécédents biologiques et environnementaux du site sont mal connus, ne présente pas alors une grande signification.

Cette remarque, ainsi que celle ci-dessous, s'applique à nos travaux antérieurs à 1985 et aux interprétations figurant implicitement ou explicitement dans ceux de nos prédécesseurs : VERHOEFF, BRÖLEMANN, HALKKA, BLOWER, FAIRHURST (cf. 1974), BAKER, ENGHOFF...

Le nombre de RO est parfois difficile à établir, notamment chez les différentes sortes de mâles adultes et d'intercalaires âgés (dimorphisme sexuel?). La détermination de l'âge se complique du fait de la possibilité de chevauchements dans un même site (mélange de stades précoces et tardifs ayant le même nombre de RO) ou dans plusieurs sites différents (rythmes différents d'un site à l'autre) (SAHLI, 1992). De plus, en mai, à l'âge d'1 an et demi, une partie des femelles est en avance d'une rangée ocellaire (et donc d'un stade) sur les mâles de la même génération : dimorphisme sexuel couramment observé.

Source : MNHN, Paris

La question de deux APA consécutives (preuve indirecte d'une itéroparité femelle importante)

Dans le sud-est de la France, nous n'avons jamais observé 2 vraies APA deux années consécutives. En revanche, il peut y avoir 2 AAA (pour les mâles : d'abord des ad1 puis, l'année suivante, des intercalaires suivis d'ad2).

Deux vraies APA , deux années consécutives, seraient la preuve tangible d'une itéroparité directe femelle, importante, dans laquelle presque toutes (≈80 %) les femelles ad1 d'une année seraient capables de pondre une nouvelle fois l'année suivante. Pareille preuve indirecte n'a jamais pu être apportée.

Admettons qu'il y ait fractionnement (stratégie CAT) et que le rapport des ad1 mâles produits 2 années consécutives soit de 50/50 (ou 10/40/40 sur 3 années consécutives). Il peut alors y avoir des adultes ad1 en plus ou moins grand nombre deux années consécutives (50/50 ou 40/40). Si les femelles ad1 et les pontes sont fractionnées dans le temps dans les mêmes proportions que celles admises ci-dessus pour les ad1 mâles, on est conduit à deux pseudo APA (50/50 ou 40/40) et non à 2 vraies APA (80 et 80). Dans le cas de deux vraies APA consécutives, il y aurait des pontes explosives deux années de suite, donc deux fois plus de pontes par année. Si la distinction entre pseudo et vraies APA est facile en théorie et en pratique dans les cas extrêmes, elle peut cependant être fort délicate lorsque les cas sont moins tranchés.

Le rôle des intercalaires

Dans le cas de Sibourg, les nombreux intercalaires du printemps 1987, des SL pour la plupart (composante α de la périodomorphose, SAHLI, 1990), ne furent très probablement d'aucune utilité et moururent sans avoir pu jouer de rôle : bien que devenus des ad2 en été 1987, les femelles (partenaires en puissance de ces ad2 mâles) ne purent probablement pas être fécondées une nouvelle fois en 1987.

A faible altitude dans le sud-est de la France et de nos jours, les rôles des intercalaires chez *O. sabulosus* peuvent être les suivants :

(a) sous la forme de SL, ils fournissent des partenaires mâles (ad2) aux femelles ad1 dans le cas d'une non-synchronisation massive des maturations mâles et femelles (décalage dans le temps, *cf. supra* le cas de la MM de Peillon),

(b) sous forme de SL (ou de LL), ils fournissent des partenaires ad2 aux femelles ad1 dans le cas où les pontes sont fractionnées dans le temps (stratégie CAT) : certaines femelles pondent l'année x, d'autres, de même génération l'année x+1, d'autres encore, de même génération l'année x+2, etc.

(c) sous la forme de SL (et/ou de LL) s'il existe encore de nos jours une itéroparité femelle indirecte ou directe.

Sur une vingtaine d'années, il est possible que les femelles fassent usage, selon les générations, les sites et l'environnement, tantôt de la possibilité (a), tantôt de la (b), tantôt de la (c), voire peut-être de combinaisons : (a) + un peu de (c) ou (b) + un peu de (c).

La présence d'abris

Lorsque surviennent de fortes pluies, les iules quittent les zones à végétation peu dense et basse (touffes d'*Euphorbia* dans le Mentonnais) pour se réfugier généralement dans des sites-abris (sites-relais), où la végétation est abondante, dense et haute, composée d'arbres, d'arbrisseaux ou de buissons protecteurs et non plus de touffes.

HALKKA (1958) avait déjà signalé de pareils déplacements chez *O. sabulosus* en Finlande : déplacements entre un site bien abrité à végétation dense et entre un site exposé à végétation clairsemée, lors de l'hivernation ou lors de pontes. De pareils déplacements ont aussi été notés par FAIRHURST (1968) en Grande-Bretagne.

Lors des migrations en masse dans les villages de Sibourg et de Peillon, les spécimens de *O. sabulosus* sont, semble-il, partis (au printemps de la MM) de sites-abris ou relais (garrigue dense de Sibourg constituée notamment de chênes, zone boisée et garrigue dense de Peillon). Ce

Source : MNHN, Paris

départ peut s'expliquer par une protection devenue insuffisante(?) ou, après les pluies, par un hygrotropisme négatif (réaction à l'égard d'une humidité trop élevée dans les sites-abris) et/ou en grande partie sous la pression démographique (énorme densité d'individus sous chaque abri).

Ils grimpent alors sur les surfaces verticales qu'ils rencontrent sur leur trajet : murs d'habitations humaines, d'églises ou de chapelles, murs de canaux, rochers verticaux, parois de tunnels autoroutiers (Sibourg), arbres (*cf. Pachyiulus*, SAHLI, 1984), oliviers notamment. Ils peuvent aussi séjourner sur des aires horizontales surélevées (tombes des cimetières de Peillon et de Gorbio).

La faible influence des prédateurs, des compétiteurs et des parasites

Il peut y avoir des prédateurs (coléopères, araignées, scorpions, sangliers?, blaireaux, renards?, scolopendres? présentes à Sibourg), des cohabitants qui ne sont pas réellement des compétiteurs (comme dans le Mentonnais *Cylindroiulus limitaneus, Trichoblaniulus hirsutus, Callipus foetidissimus* ou *Glomeris sp.* dans certains sites : leur rôle est vraisemblablement négligeable). Des parasites tels que les larves de certains diptères peuvent jouer un rôle important. Toujours est-il que : (a) le nombre des individus devenus adultes en 1984 a été considérable ; (b) les individus nés en automne 1984 de pontes extraordinairement importantes sont, pour une bonne part, devenus adultes en 1986 ou 1987, l'influence des prédateurs, concurrents, et parasites ayant été faible ou nulle.

On peut supposer que le nombre d'individus parvenus à l'état adulte (ad1) à partir de chaque ponte a été exceptionnellement supérieur en 1984 puis en 1986 (Sibourg) et en 1987 (Peillon) au nombre habituel (à partir de plusieurs centaines d'oeufs d'une ponte, une fraction importante de larves meurt habituellement au cours du développement).

La proximité d'une vaste garrigue

Dans le sud-est de la France il est logique de penser qu'une MM ne peut se produire que lorsqu'une vaste garrigue permet l'hébergement, puis le déplacement, d'un nombre considérable d'individus. De Salon-de-Provence à Aix-en-Provence, la garrigue s'étend sur des kilomètres : les sites à *O. sabulosus* sont étendus. On ne saurait imaginer un important déplacement à partir d'un îlot de garrigue ou d'une zone ne comportant que de petits fragments de garrigue, comme c'est le cas dans nombre des stations du Mentonnais : ici, à part Peillon, peu de sites peuvent constituer un terrain favorable à une MM avec invasion. A Peillon, la MM a été de moindre envergure qu'à Sibourg, sans doute parce que l'étendue du site à *O. sabulosus* y est moindre.

Une MM avec invasion d'habitations ne se produit que lorsque un village est implanté dans la garrigue, à proximité d'une garrigue assez vaste, ou sur l'itinéraire d'un déplacement. Dans l'état actuel de nos connaissances, on ne saurait imaginer une MM dans de grandes agglomérations comme celles de Nice, Monaco ou Menton. Dans le Mentonnais, les endroits les plus exposés à une future MM avec invasion, outre Peillon, nous paraissent être le hameau d'Engarvin et les villages de Gorbio et de Sainte-Agnès. Dans ces deux derniers, une mini-invasion de murs d'habitations par *O. sabulosus* eut lieu non au printemps mais, paradoxalement, en automne 1988 après des pluies.

Pourquoi une MM n'a-t-elle pas eu lieu en 1985 ?

1984 ayant été une année exceptionnelle tant par l'abondance d'individus matures (AAA) que par celle de pontes (APA, automne 1984), comment se fait-il qu'il n'y ait pas eu de MM, ni en Provence (Sibourg), ni dans les Alpes-Maritimes (Peillon) l'année suivante, au printemps 1985? Pourtant les conditions d'une double surpopulation SIN+SJL étaient remplies au printemps 1985 comme au printemps 1987 à Sibourg.

Trois différences méritent d'être signalées:

Source : MNHN, Paris

a) hiver 1984-1985 exceptionnellement froid, que les jeunes larves et les adultes, bien adaptés, ont remarquablement supporté, même en altitude (observations personnelles);

b) sécheresse inhabituelle du printemps 1985 et du printemps 1986 ;

c) surpopulation SIN (grands individus) du printemps 1985 sans doute moindre que celles des printemps 1986 et 1987 à Sibourg : la composante IN de 1986 (puis de 1987) a probablement été amplifiée par rapport à celle de 1984 ; en effet chaque femelle ad1 de 1984 a produit plusieurs centaines d'oeufs devenus, *pro parte,* à leur tour, des ad1 en 1986 (Sibourg), augmentant ainsi le nombre des IN de 1986 (devenus des post-adultes en 1987) par rapport à ceux de 1984 (*cf. supra*).

En 1985, la sécheresse a pu maintenir les populations de *O. sabulosus* dans leur habitat (notamment les jeunes larves) empêchant toute émigration. Il n'y a eu en effet nulle part de MM avec invasion. Nous émettons l'hypothèse que l'absence de pluie est responsable d'une absence de MM même en cas de surabondance des individus post-imaginaux et des jeunes larves. Peut-être aurait-il suffi de quelques pluies légères au printemps 1985 pour déclancher des MM à certains endroits. Aussi admettrons nous que les pluies sont une condition déterminante de MM.

CONCLUSION

Là où il y a eu des invasions, les habitations humaines sont typiquement construites dans des sites à iules, souvent très anciens : ainsi en Sarre, en 1973, en Yougoslavie en 1984, dans les Alpes-de-Haute-Provence en 1989 (*Cylindroiulus broti*, d'après SAHLI, inédit), dans divers sites des Bouches-du-Rhône et à Peymenade dans les Alpes-Maritimes en 1963 (SAHLI, inédit). C'est un peu comme si on avait bâti sur une termitière ou sur une fourmillière, ou à proximité. Vouloir goûter les joies de vivre en pleine nature, mais n'en supporter aucune conséquense est difficilement conciliable. Le corollaire de notre affirmation est qu'il existe des déplacements massifs de *O. sabulosus* sans invasions, passant totalement inaperçus lorsque les habitations font défaut. Nous en avons observé dans le Mentonnais à Rocca Spaviera et au Pas de l'Escous. Le cas décrit par VERHOEFF en Alsace trouve sa place dans cette rubrique dans la mesure où les *O. sabulosus* ont simplement traversé une voie ferrée.

Le fait de grimper sur les murs les parois d'un canal traduit, dans un premier temps, une réaction de fuite ou un hygrotropisme négatif. Dans le cas d'une surpopulation, concernant les femelles ad1 ayant pondu l'automne précédent, ce comportement conduit, dans un deuxième temps, à une mortalité considérable. Fixés sur des murs, les iules semblent ne pas se nourrir et s'exposent à la déshydratation. Or, dans le Sud-Est, en avril et mai, l'alimentation est nécessaire à la production des œufs chez les femelles, à la mue intercalaire 1- ad2 des mâles en vue de l'accouplement.

Des essais d'invasion expérimentale ont été conduits à l'intérieur et à l'extérieur (balcons) de plusieurs immeubles du Mentonnais (*O. sabulosus*) ainsi que sur un balcon dans un appartement à Dijon (*O. sabulosus* et *Tachypodoiulus niger*) : les animaux, inoffensifs, sont morts au bout de quelques jours.

Les invasions massives suivies de déplacements et d'une forte mortalité traduisent vraisemblablement une régulation des populations. En effet, si tous les animaux adultes et intercalaires qui migrent massivement au printemps se reproduisaient dans le même site en automne (ad2 mâles et femelles), les ressources alimentaires deviendraient vite insuffisantes. La surpopulation doit logiquement conduire à coloniser des sites nouveaux ou moins peuplés, à condition que la chose soit possible compte tenu, par exemple, de l'anthropisation croissante des milieux. À notre connaissance, il n'existe pas encore, en Europe, de sites envahis massivement deux années consécutives.

Il convient de dire que les invasions massives de iules constituent un risque périodique dans tout le sud-est de la France, au mois d'avril et en été, voire en début d'automne, pour certains équipements (autoroutes A8 et A9,...) et habitations.

Source : MNHN, Paris

RÉFÉRENCES

BAKER, G. H., 1978a. — The distribution and dispersal of the introduced millipede *Ommatoiulus moreletii* (Diplopoda: Julidae) in Australia. *J. Zool. Lond.*, **185** : 1-11.

BAKER, G. H., 1978b. — The post-embryonic development and life history of the millipede *Ommatoiulus moreletii* (Diplopoda : Julidae) introduced in south-eastern Australia. *J. Zool. Lond.*, **186** : 209-228.

BAKER, G. H., 1978c. — The population dynamics of the millipede *Ommatoiulus moreletii* (Diplopoda: Julidae). *J. Zool. Lond.*, **186** : 229-242.

BAKER, G. H., 1979. — The activity patterns of *Ommatoiulus moreletii* (Diplopoda: Julidae) in South Australia. *J. Zool. Lond.*, **188** : 173-183.

BAKER, G. H., 1984. — Distribution, morphology and life history of the millipede *Ommatoiulus moreletii* (Diplopoda: Julidae) in Portugal and comparisons with Australian populations. *Aust. J. Zool.*, **32** : 811-822.

DEMANGE, J. M., 1960. — Sur un important rassemblement de *Schizophyllum sabulosum* (L.). *Cah. Natural. Bull. nat., Paris*, **16** : 89-91.

DEMANGE, J. M., 1963. — *Myriapodes. In* : Encyclopédie de la Pléiade, *Zoologie II, Les Arthropodes*. Paris, Gallimard : 411-486.

DEMANGE, J. M., 1981. — *Les Millepattes. Myriapodes*. Paris, Boubée, 284 pp.

HALKKA, R., 1958. — Life-history of *Schizophyllum sabulosus* (L.) (Diplopoda, Iulidae). *Ann. Zool. Soc. Zool. Bot. Fenn. "Vanamo"*, **19** : 1-72.

HELB, H. W., 1975. — Zum Massenauftreten des Schnurfüssers *Schizophyllum sabulosum* im Saarland (Myriapoda: Diplopoda). *Entomologica,* Stuttgart, Fischer Verlag.

FAIRHURST, C. P., 1968. — Life cycles and activity patterns of schizophylline millipedes. Ph. D. Thesis, University of Manchester, 407 pp.

FAIRHURST, C. P., 1969. — Activity and wandering in *Tachypodoiulus niger* (Leach) and *Schizophyllum sabulosum* (L.). *Bull. Mus. nat. Hist. nat. Paris*, **41, suppl. 2** : 61-66.

FAIRHURST, C. P., 1974. — The adaptive significance of variations in the life cycles of schizophylline millipedes. *Symp. zool. Soc. Lond* , **32** : 575-585.

SAHLI, F., 1984. — Quelques exemples de déplacements en masse et de rassemblements chez les Myriapodes Diplopodes. *109ème Congr. nat. Soc. savantes, Dijon, sc. II* : 253-261.

SAHLI, F., 1986a. — On some roles of periodomorphosis in *Ommatoiulus sabulosus* (L.) (Myriapoda, Diplopoda) in the Maritime Alps. *In* : PORCHET, *Advances in Invertebrate Reproduction , 4* . Elsevier Sc. Publ. : 409-416.

SAHLI, F., 1986b. — Fréquence de la périodomorphose chez le Diplopode Julide *Ommatoiulus sabulosus* (L.) dans les Alpes-Maritimes. I. Passages mâle adulte-mâle intercalaire dans des élevages effectués in natura. *C. R. Acad. Sc. Paris, sér. III*, **302** : 679-682.

SAHLI, F., 1986c. — Influence des orages sur certains déplacements d'*Ommatoiulus sabulosus* (L.) (Myriapoda, Diplopoda, Julida) dans les Alpes-Maritimes. *Bull sci. Bourgogne,* **38** : 55-57.

SAHLI, F., 1990a. — Recherches sur le cycle des mâles et la fréquence des intercalaires d'*Ommatoiulus sabulosus* (Myriapoda, Diplopoda, Julidae) en Bourgogne. Inversion expérimentale du nombre des intercalaires et des adultes en automne. *Bull. sci. Bourgogne*, **45** : 51-59.

SAHLI, F., 1990b. — On post-adult moults in Julida (Myriapoda, Diplopoda). Why do periodomorphosis and intercalaries occur in males? *In* : A. MINELLI, *Proc. 7th Intern. Congr. Myriapodology.* Leiden, Brill : 135-156.

SAHLI, F., 1991a. — Recherches sur le cycle des mâles d'*Ommatoiulus sabulosus* (L.) (Myriapoda, Diplopoda, Julidae) dans les Alpes-Maritimes et en Provence. Remarques sur les rapports entre la périodomorphose et l'altitude. *Bull. sci. Bourg.,* **44** : 33-39.

SAHLI, F., 1991b. — Fréquence de la périodomorphose chez le Diplopode Julide *Ommatoiulus sabulosus* (L.) dans les Alpes-Maritimes et en Provence : II. Passages mâles intercalaires - mâles adultes. *Bull. sci. Bourg.*, **44** : 41-47.

SAHLI, F., 1991c. — Augmentation et production expérimentales de mâles intercalaires chez des Diplopodes Julida. Note préliminaire. *C. R. Acad. Sci. Paris, Sér. III*, **313** : 59-63.

SAHLI, F., 1992. — On male reproduction strategies in *Ommatoiulus sabulosus* (L.) in the Maritime Alps and Provence (France): juvenile to adult maturation moults. *Ber. nat.-med. Verein, Innsbruck*, **suppl. 10** : 167-176.

SAHLI, F., 1993. — Signification de la périodomorphose et des intercalaires mâles et femelles chez les Diplopodes Blaniulides cavernicoles pyrénéens. *Mém. Biospéol.,* **20** : 209-215.

VERHOEFF, K. W., 1900. — Wandernde Doppelfüssler Eisenbahnzuge hemmend. *Zool. Anz.,* **23** : 465-473.

VERHOEFF, K. W., 1921a. — Chilognathen Studien. *Arch. Naturgesch.*, **86A** : 23-80.

VERHOEFF, K. W., 1921b. — Ueber Diplopoden der Riviera und einige alpenländische Chilognathen. *Arch. Naturgesch.*, **87** : 1-110.

Source : MNHN, Paris

Distribution Patterns and Qualitative Composition of the Centipede Fauna in Forestal Habitats of Mainland Greece

Marzio ZAPPAROLI

Dipartimento di Protezione delle Piante, Università della Tuscia, 01100 Viterbo, Italy

ABSTRACT

A preliminary overview of the centipede communities inhabiting the main forestal ecosystems of mainland Greece is presented. The study is based on data collected during the last fifteen years. The literature records are thus included, after a critical evaluation from both faunistic and taxonomic point of view. 54 species are considered. The following forms of forest vegetation are considered: sclerophyllous forests (*Pistacia* spp., *Quercus coccifera*) and their stages of degradation, deciduous oakwoods (*Quercus* spp.), firwoods (*Abies cephalonica*) and beech-fir forests (*Fagus* spp., *Abies* sp. gr. *alba*). The centipede community of each formation is discussed from a faunistical, ecological and zoogeographical point of view.

RÉSUMÉ

Modalités de la répartition et composition spécifique de la faune des chilopodes des milieux forestiers de la Grèce continentale.

Ce travail présente un premier bilan des peuplements de chilopodes occupant les principaux écosystèmes forestiers de la Grèce continentale. L'étude est basée sur les données réunies durant ces quinze dernières années. Les données de la littérature accessibles sont revues de manière critique à la fois du point de vue faunistique et du point de vue taxinomique et incluses dans ce bilan. On a pris en considération les formations forestières suivantes : forêts sclérophylles (*Pistacia* spp., *Quercus coccifera*) et leurs stades de dégradation, forêts décidues de chênes (*Quercus* spp.), sapinières (*Abies cephalonica*) et hêtraies-sapinières (*Fagus* spp., *Abies* sp. gr. *alba*). Le peuplement de chilopodes de chaque formation est examiné du point de vue faunistique, écologique et zoogéographique.

INTRODUCTION

The main works published to date on the ecology of centipede communities in the Mediterranean region deals only with some South-European areas, such as Spain (SERRA, 1978; SERRA & ASCASO, 1990) and Italy (MINELLI & IOVANE, 1987; ZAPPAROLI, 1992). No data are available for North-African and East-Mediterranean countries. The aim of this paper is to give a first qualitative picture of the centipede communities in the main forest habitats of mainland Greece, in order to characterize these habitats and to allow for synecological comparisons over the Mediterranean area.

ZAPPAROLI, M., 1996. — Distribution patterns and qualitative composition of the centipede fauna in forestal habitats of mainland Greece. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 599-605. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

MATERIAL AND METHODS

In the present study the territory of Greece is considered as it is politically constituted today; the Egean Islands and Crete are not analysed. The analysis is mainly based on data collected in the last fifteen years (ZAPPAROLI, 1994), but all available literature records, critically reviewed both from faunistic and taxonomic point of view, are also included. About 280 sites are considered, 87 of which are known in their main vegetation features. 54 species of centipedes are considered: i-e about the 85% of the species occurring in the studied area and 67% of the whole Greek centipede fauna.

The discussion follows an ideal ecological-altitudinal sequence, principally according to DEBAZAC & NAVROMMATIS (1971), from the Mediterranean belt up to the higher mountain areas. The following forms of forest vegetation, loosely named from their dominant plant species, are distinguished: sclerophyllous broadleaved forests with *Pistacia lentiscus*, *Quercus coccifera* and *Quercus ilex* and their stages of degradation; deciduous thermophilous and mesothermophilous oakwoods dominated by *Quercus* spp.; coniferous woods with *Abies cephalonica*; broadleaved woods with *Fagus* spp. and *Abies* sp. gr. *alba*. The centipede community of each vegetation type is discussed from the faunistical and zoogeographical point of view; both general and local features are pointed out; characteristic species are also tentatively suggested.

In Table 1 the species are listed according to their presence/absence in the four habitats considered; the altitudinal ranges are tentative; chorotypes have been established according to VIGNA *et al.* (1992). SS = evergreen sclerophyllous formations; QQ = thermophilous and mesothermophilous broadleaved woods dominated by *Quercus* spp.; AC = woods dominated by *Abies cephalonica*; FF = broadleaved woods dominated by *Fagus* spp. and *Abies* spp. gr. *alba*. Chorotypes as follows: cae = Centroasiatic-european, eur = European, seu = S-European, sie = Sibiric-european, med = Mediterranean, tem = Turanic-european-mediterranean, tum = Turanic-mediterranean, wmd = W-Mediterranean.

RESULTS

Evergreen mediterranean sclerophyllous forests

These forests are physionomically characterized mainly by evergreen shrubs of woods. The most important species are *Pistacia lentiscus*, *Juniperus phoenicea*, *Ceratonia siliqua,* in the thermorphilous sites, between 0-600 m a.s.l., *Quercus coccifera* and *Phillyrea media*, mostly in more inland sites up to 1000-1200 m, while *Q. ilex* occurs in relatively mesophilous sites, from the sea level up to 650-800 m. Open habitats, such as phrygana, mainly derived from human activities (fire, grazing, cutting) in the Mediterranean forest, are related to the sclerophyllous formations. These habitats are especially characterized by *Cistus* spp., *Phlomis* spp. and *Sarcopoterium spinosum*. Sclerophyllous forests occur especially in Peloponnese and in Thessaly, but are also present in Macedonia, in Central Greece and in Thrace.

The general features of the centipede communities in the sclerophyllous and related open habitats of the whole mainland Greece are mostly characterized by very common widespread Mediterranean species such as *Scolopendra cingulata* and *Scutigera coleoptrata*, both invasive, the E-Mediterranean *Pleurolithobius patriarchalis*, and the S-European *Eupolybothrus litoralis*. Besides, *Bothriogaster signata*, widespread from Turan to E-Mediterranean steppes, *Himantarium gabrielis*, Mediterranean, and *Stigmatogaster gracilis*, S-European, inhabits especially open habitats. However, all these species are euriecious and occur also in disturbed or thermophilous broadleaved oakwoods and firwoods, up to 2000-2100 m a.s.l.

In the sclerophyllous formations of W-Greece, the above mentioned species are locally accompanied by the E-Mediterranean *Henia hirsuta*, *Nannophilus ariadnae*, *Scolopendra dalmatica* and the S-European *Lithobius hauseri*, all ranging between 0 and 900 m a.s.l. *H. hirsuta* is endemic to Epirus; *N. ariadnae* is recorded from Kerkira, Crete and Karpathos; *S. dalmatica* ranges from Greece to Istria along the Adriatic Sea coasts; *L. hauseri* is only known from Kerkira. In the phrygana of the Ionian Islands *Cryptops trisulcatus* is also present, mainly in thermophilous habitats of W-Mediterranean regions. Otherwise, this species has been recorded in Greece only from the S-Sporades, no mainland records are to date known and it is possible that the Ionian and Egean populations both result from introductions. In evergreen formations of W- and S-Greece the Mediterranean *Dignathodon microcephalum* and *H. bicarinata* have also been recorded. In E-Greece, characteristic Lithobiids occuring in sclerophyllous open habitats of Attica and W-Peloponnese are *L. carinatus*, widespread from Palestine to Greece, and *L. nigripalpis*, SE-European.

Source : MNHN, Paris

TABLE 1. — Centipedes from forestal habitats of mainland Greece (* = present, - = absent): species are grouped according to their ecological affinities. m = altitudinal range; C = chorotypes. Abbreviations & explanations in the text (Material & methods).

Species/habitats	SS	QQ	AC	FF	m	C
Stigmatogaster gracilis (Meinert)	*	-	-	-	0-500	seu
Dignathodon microcephalum (Lucas)	*	-	-	-	0->?	med
Henia bicarinata (Meinert)	*	-	-	-	0-1000	med
H. hirsuta Verhoeff	*	-	-	-	0-300	emd
Nannophilus ariadnae Attems	*	-	-	-	0-300	emd
Cryptops trisulcatus Brölemann	*	-	-	-	0-350	med
Scolopendra dalmatica C. L. Koch	*	-	-	-	0-900	emd
Lithobius carinatus L. Koch	*	-	-	-	0-800	emd
L. hauseri (Dobroruka)	*	-	-	-	0-500	seu
L. agilis C. Koch	*	*	-	-	200-1200	eur
Pleurolithobius patriarchalis (Berlese)	*	*	-	-	100-1100	emd
Bothriogaster signata (Kessler)	*	*	*	-	0-1700	tum
Henia devia C. L. Koch	*	*	*	-	0-1800	emd
Geophilus carpophagus Leach	*	-	-	-	50->?	eur
Pleurogeophilus mediterraneus (Meinert)	*	-	*	-	0-2100	seu
Scolopendra cingulata Latreille	*	*	*	-	0-2350	med
Scutigera coleoptrata (Linné)	*	-	*	-	0-1100	med
Eupolybothrus litoralis (L. Koch)	*	*	*	-	0-2200	seu
Lithobius brignolii (Matic)	*	-	*	-	800-1800	seu
L. microps Meinert	*	-	*	-	200-1700	seu
L. nigripalpis L. Koch	*	*	*	-	0-2500	seu
Pleurolithobius orientis (Chamberlin)	*	-	*	-	200-1100	emd
Lithobius muticus C. L. Koch	-	*	*	-	750-2200	ceu
Geophilus insculptus Attems	-	-	*	-	1900-2100	eur
Lithobius tenebrosus Meinert	-	-	*	-	1400-1500	eur
Geophilus linearis C. L. Koch	-	*	-	*	400-1900	eur
Lithobius crassipes L. Koch	-	*	*	*	600-1500	eur
L. latro Meinert	-	*	*	*	600-2000	seu
L. microps sensu AA.	-	*	*	*	300-1200	eur
L. peregrinus Latzel	-	*	*	*	800-1500	seu
Strigamia engadina (Verhoeff)	-	-	*	*	1100-2100	ceu
Cryptops anomalans Newport	-	-	*	*	500-2000	eur
Eupolybothrus transsylvanicus (Latzel)	-	-	*	*	700-1850	seu
E. werneri (Attems)	-	-	*	*	700-2300	sue
Lithobius lucifugus L. Koch	-	-	*	*	1200-2400	ceu
L. mutabilis L. Koch	-	-	*	*	1000-2000	ceu
L. schuleri Verhoeff	-	-	*	*	1200-2000	seu
Schendyla montana Attems	-	-	-	*	1200-1500	seu
Clinopodes trebevicensis (Verhoeff)	-	-	-	*	500-2200	seu
Strigamia transsilvanica (Verhoeff)	-	-	-	*	1150-1250	seu
Lithobius beschkovi Matic & Golemansky	-	-	-	*	1400	seu
L. lakatnicensis Verhoeff	-	-	-	*	1100	seu
Himantarium gabrielis (Linné)	*	*	*	*	0-1900	med
Henia athenarum Pocock	*	-	*	*	0-1300	emd
H. illyrica (Meinert)	?	*	*	*	0-2100	ceu
Clinopodes flavidus C. L. Koch	*	*	*	*	0-2400	cae
Pachymerium ferrugineum (C. L. Koch)	*	*	*	*	0-2300	tem
Cryptops hortensis Leach	*	*	*	*	200-1450	eur
C. parisi Brölemann	*	*	*	*	400-2400	eur
Eupolybothrus caesar (Verhoeff)	*	*	*	*	300-2100	seu
Harpolithobius anodus (Latzel)	*	-	*	*	0-2100	seu
Lithobius erythrocephalus C. L. Koch	*	*	*	*	150-2900	eur
L. lapidicola Meinert	*	*	*	*	100-2400	eur
L. viriatus Sseliwanoff	*	*	*	*	200-2400	seu
N° species (54)	33	23	36	29		

Source : MNHN, Paris

33 species altogether have been recorded from Greek sclerophyllous woodlands, and 9 of them seem to be exclusive of such habitats. The number of species in some *Q. coccifera* stands of Epirus, Macedonia and Central Greece (Ioannina, Amphitea; Kavala, Palea Kavala; Fthiotida, Purnari) range between 9-10. Under more thermophilous conditions, such as in *Pistacia lentiscus* shrubs or in phrygana, the number is much lower, with no more than 4-5 species (Evia, Nea Artaki).

Thermophilous and mesothermophilous broadleaved oakwoods

Greece oakwoods are mainly dominated by *Quercus pubescens*, *Q. cerris*, *Q. frainetto*, *Q. petrea*; other broadleaved species such as *Castanea sativa* and *Ostrya carpinifolia* may also be associated with. These formations are mainly distributed in Thrace, Thessaly and Macedonia, from low altitudes; the extend but marginally to Peloponese, where they are mainly restricted to the mountain areas.

The centipede communities of these woods are not easy to characterize: these habitats are heavily influenced by human activities which have affected both floristic composition and geographic distribution. Besides, faunistic and ecological data are still few. A large number of very euriecious species, widespread in European and in W-Paleartic regions, such as *Clinopodes flavidus*, *Pachymerium ferrugineum*, *Cryptops hortensis*, *Lithobius erythrocephalus*, *L. lapidicola*, has been recorded from Greek oakwoods. Species mostly common in the adjacent vegetation types, such as *Pleurolithobius patriarchalis* and *L. nigripalpis*, especially related to the sclerophyllous formations, or *Pleurogeophilus mediterraneus* and *L. brignolii,* more linked to the *Fagus* or *Abies cephalonica* woods, are also present. In oakwoods of Northern regions, we can find European or S-European species such as *Geophilus linearis*, *L. crassipes, L. peregrinus*, *L. microps* sensu auct., *L. viriatus*, also present in coniferous or in mesophilous broadleaved forests. In the mesothermophilous oakwoods sites of Epirus occur the S-European *Eupolybothrus caesar*, but it lives also in the beech-fir forest of the same area.

To date 23 species of centipedes have been recorded altogether from Greek oakwoods, but this value it is probably underestimated. No exclusive species are known. The number of centipede species recorded in some *Quercus* stands in N-Greece ranges from 6 (Kastoria, Gavros) to 9 (Garakas, Xanthi).

Coniferous woods dominated by Cephalonian fir and mesophilous decidous broadleaved woods dominated by beech and fir

Owing to their relative faunistic homogeneity, the centipede communities of the two most important forestal habitats of mountain areas in Greece are discussed together.

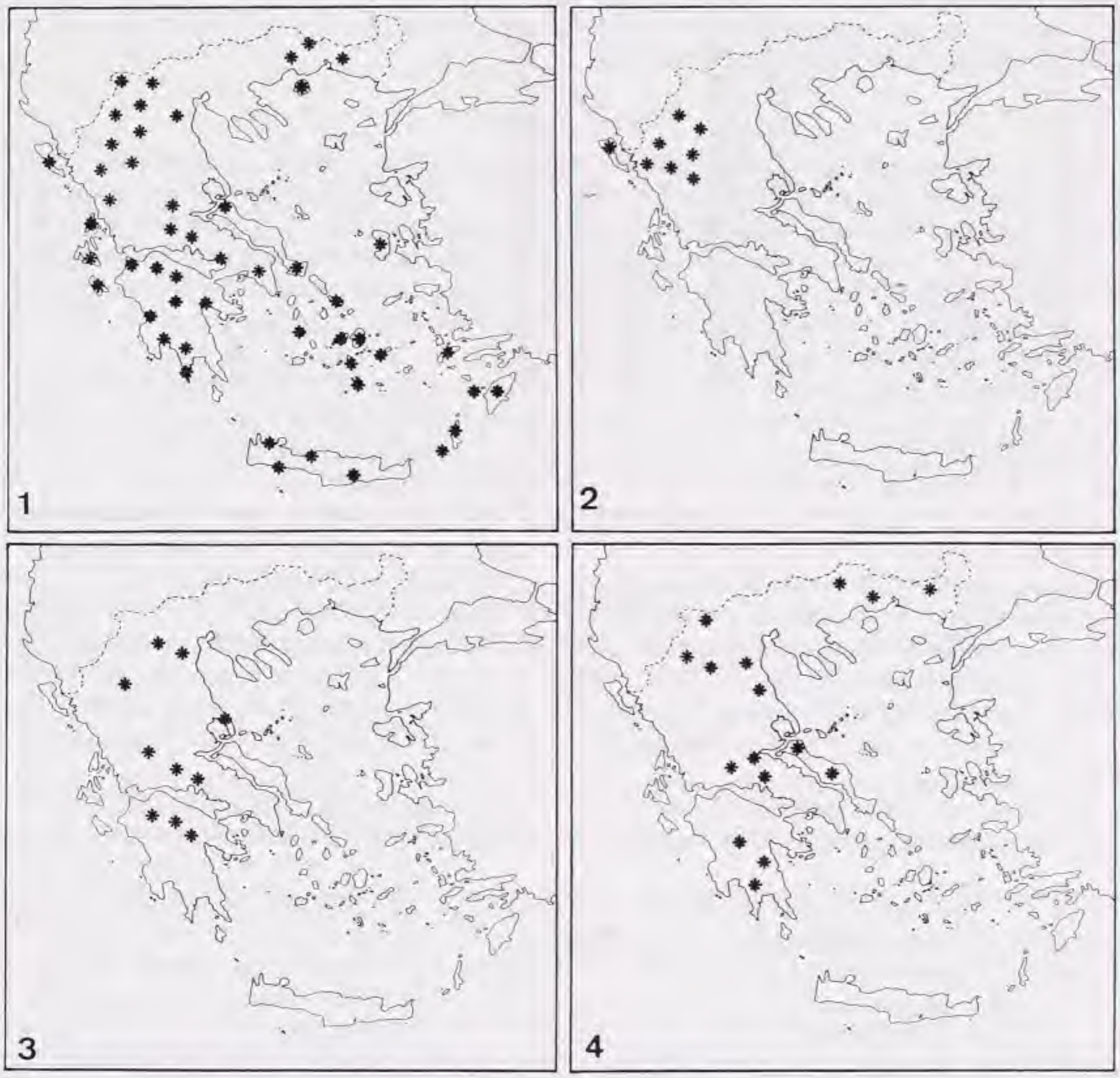
Firwoods, dominated by the endemic *Abies cephalonica*, are characteristic of the Peloponnese, Attica and Central Greece, mainly between 550-2000 m a.s.l., according to the exposure. *Pinus nigra* is sometimes mixed with Cephalonian fir.

Fagus (*F. sylvatica*, *F. orientalis*) and *Abies* (*A*. spp. gr. *alba*) woods are mostly distributed in the Northern regions, along the Pindus, in E-Thessalia and N-Macedonian along the Mt. Rodopi. Beech and fir forests are also in Chalcidice and in Mt. Pangeo. Such formations generally begin from 850-1000 m a.s.l., but exceptionally (Chalcidice) they may be present from 200 m a.s.l. In these forests, the presence of the beech progressively increases from South to North, whereas that of *Abies* relatively decreases.

The main qualitative features of the centipede communities in Cephalonian firwoods and in beech-firwoods is largely similar. 42 species altogether have been recorded and about the 55% of these are recorded in both habitats. Many of the species recorded in such formations are widespread all over Europe, such as *Cryptops anomalans*, in Central Europe, or *Strigamia engadina*, *Lithobius lucifugus* and *L. mutabilis* or in SE-Europe, *Eupolybothrus werneri* and *L. schuleri*. The S-European *E. transsylvanicus* also inhabits *Fagus* woods as well Southernmost

Source : MNHN, Paris

A. cephalonica stands but Northern populations are morphologically distinguishable from Southernmost ones (Central Greece, Eubea, Peloponnese) (ZAPPAROLI, 1994). A relatively larger stock of Mediterranean species characterizes the *A. cephalonica* forests, up to 2000 m. In the Northernmost *Fagus* woods European especially S-European species, tend to predominate. However, Mediterranean species, such as *Himantarium gabrielis*, *Henia athenarum*, *Scolopendra cingulata*, are also present in Mt. Pangeo (Thracia) beechwoods, especially in the open and lowest sites of the Southern slopes.



FIGS 1-4. — Distribution of *Eupolybothrus* species in Greece : *E. litoralis* (1), *E. caesar* (2), *E. werneri* (3), *E. transsylvanicus* (4).

Lithobius tenebrosus, widespread in Europe, seems to be the main characteristic species under Cephalonian firwoods, ranging between 1100-2300 m. Five species seem to be characteristic of the beechwoods sites: *Schendyla montana*, *Clinopodes trebevicensis*, *Strigamia*

Source : MNHN, Paris

transsilvanica, *Lithobius lakatnicensis*, all distributed in S-Europe and up to date recorded in Greece only from Macedonia and Thracia, between 1100-1250 m a.s.l., and *L. beschkovi*, to date known from Macedonian. *L. lakatnicensis* is also known only from S-Bulgarian caves and closely related species are present in European Turkey. In N-Greece beechwoods it is also present *L. erythrocephalus borisi*, a race also known from SW-Bulgaria.

The number of species recorded in *Abies cephalonica* woods seems to be higher as compared to the other forestal types: 36 species have been sampled altogether but only one seems to be exclusive of this vegetation type. In Peloponnese (Mt. Killini, Mt. Taigetos) and in Central Greece (Mt. Parnasus) firwoods stands 13-17 species have been recorded. In Greek beechwoods, 29 species have been recorded altogether and 6 species seem to be exclusive. In some Macedonian *Fagus* woods (N-Pindus, Mt. Falakrö) 8-11 species have been recorded, whereas 10 species are at least present in Mt. Olimpos beechwoods and 18 species have been recorded in Katara Pass (Pindus) beechwoods.

CONCLUSION

Data on Chilopoda in forestal habitats of mainland Greece are still fragmentary and both qualitative and quantitative information is needed to reach adequate knowledge, especially of thermophilous and mesothermophilous oakwoods communities. Difficulties in drawing a complete picture also rise from the still incomplete faunistical and taxonomical knowledge of the Greek fauna. Besides, because of the heavy human impact that affects the S-Balkans forestal landscape, especiallay at the lower altitudinal sites, it is sometimes difficult to assess the original features of animal communities.

However, according to the preliminary data discussed in this contribution, the centipede communities inhabiting in the forestal habitat of Greece seem to show a qualitative composition characteristic and well related to the main bioclimatic and microclimatic conditions. Some indicators of different conditions could be recognized. Among Lithobiidae, the four Greek species of the S-European genus *Eupolybothrus* (Figs 1-4), well known both from taxonomic and faunistic point of view (ZAPPAROLI, 1994), could be tentatively used. According to their geographical distribution and habitat preferences, they can be listed according to a decreasing thermophilic sequence: *E. litoralis* present in a wide range of thermophilous habitats in mainland as well as in insular Greece from the sea level; *E. caesar* only inhabiting the thermophilous and mesothermophilous sites of Epirus from 300 m a.s.l.; *E. transsylvanicus* and *E. werneri* in mountain forestal habitats under *A. cephalonica* as well as *Fagus*, both from 700 m. The last three species do not occur in the Southernmost xerothermic areas such as Attika and Egean Islands.

The analysis of the chorotypes represented in the centipede fauna altogether recorded in each forestal habitat gives further useful informations to describe these communities (see Fig. 5).

The European s.l. species are the most important group in all forestal habitats of mainland Greece, their relative importance ranging from about 48% in sclerophyllous forest up to 90% in mesophilous *Fagus* woods. Species mainly ranging in S-Europe show, among the European s.l., the highest percentage in all habitats investigated and are dominant also in the more thermophilous biotopes (30%). The percentage of the Mediterranean s.l. species is high only in the mainland sclerophyllous forests (42%) whilst it is very low in the other forestal habitats (13% on an average). The E-Mediterranean group is the main among the Mediterranean s.l. species in sclerophyllous forests (24%). W-Palearctic species are poorly represented in all studied forestal habitats and they show similar percentages (9% on an average). A decrease of the percentage of the Mediterranean s.l. species accompanied by a progressive increase of the European s.l. species is clearly observed following the ecological sequence from the sclerophyllous ecosystems to the mesophilous beechwoods.

Source : MNHN, Paris

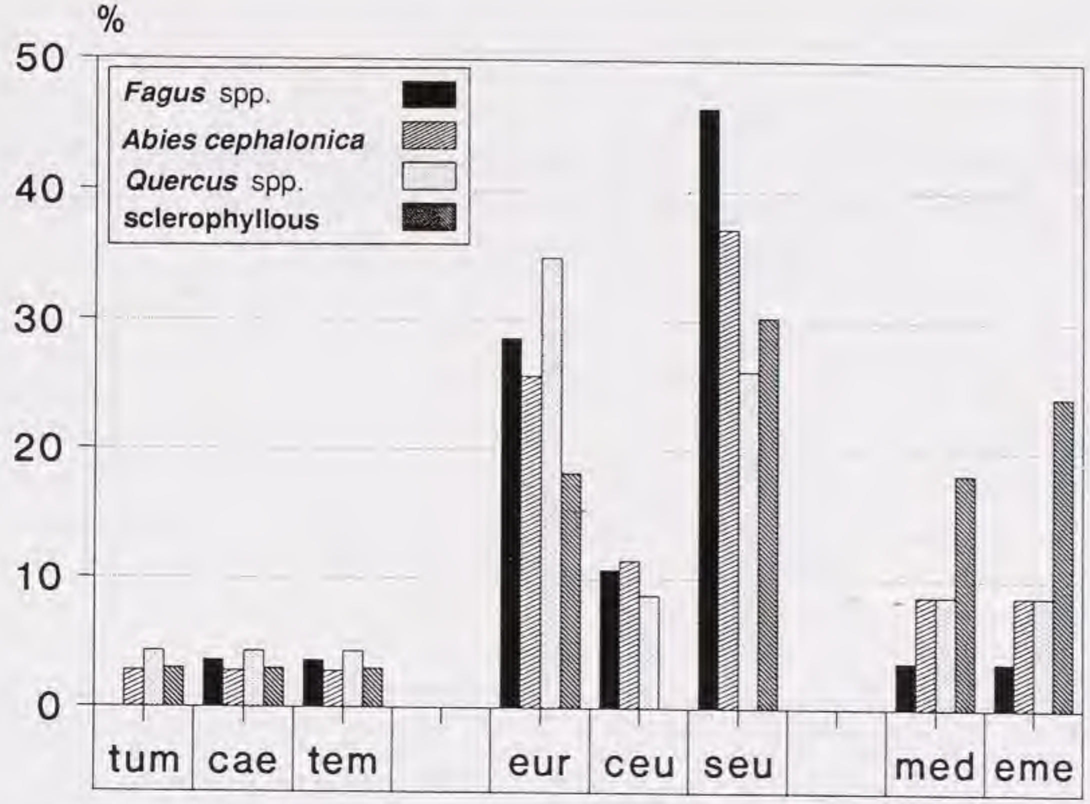


FIG. 5. — Chorotypes (%) represented in centipede communities of forestal habitats of mainland Greece. See Table 1 for abbreviations.

ACKNOWLEDGEMENTS

This research of the Zoological Institutes of Roma Universities in the Near East (n° 173) has been supported by a grant of the CNR.

REFERENCES

DEBAZAC, E. F. & MAVROMMATIS, G., 1971. — Les grandes divisions écologiques de la végétation forestière en Grèce continentale. *Bull. Soc. bot. Fr.*, **118** : 429-452.

MINELLI, A. & IOVANE, E., 1987. — Habitat preferences and taxocenoses of Italian centipedes (Chilopoda). *Boll. Mus. civ. St. nat. Venezia*, **37** (1986) : 7-34.

SERRA, A., 1978. — Contribution al conocimiento de los quilopodos de algunas zonas aridas de la peninsula iberica. Los Monegros (Aragon). *Misc. Zool.*, **4** : 31-42.

SERRA, A. & ASCASO, C., 1990. — Analisis de la composicion faunistica y variacion estacional de los Quilopodos de tres habitats del Montseny (Cataluña) capturados con trampas de caida. *In* : A. MINELLI, *Proc. 7th Int. Congr. Myriapodology*, Leiden, Brill : 385-401.

VIGNA TAGLIANTI, A., AUDISIO, P. A., BELFIORE, C., BIONDI, M., BOLOGNA, M. A., CARPANETO, G. C., DE BIASE, A., DE FELICI, S., PIATTELLA, E., RACHELI, T., ZAPPAROLI, M. & ZOIA, S., 1992. — Riflessioni di gruppo sui corotipi fondamentali della W-paleartica ed in particolare italiana. *Biogeographia*, **16** : 159-179.

ZAPPAROLI, M., 1992. — I Chilopodi negli ambienti forestali italiani. *Monti e Boschi*, **5** : 1-12.

ZAPPAROLI, M., 1994. — Note tassonomiche e faunistiche su Chilopodi della Grecia continentale ed insulare (Chilopoda). *Fragm. Entomol.*, **26** : 11-66.

Source : MNHN, Paris

Source : MNHN, Paris

On Abundance, Phenology and Natural History of Symphyla from a Mixedwater Inundation Forest in Central Amazonia, Brazil

Joachim* ADIS *, *José Wellington de* MORAIS ** & *Ulf* SCHELLER **

* Max-Planck-Institute for Limnology, Tropical Ecology. Working Group, Postfach 165, D-24302 Plön, Germany
** Instituto Nacional de Pesquisas da Amazônia (INPA), C.P. 478, 69.011-970 Manaus/AM, Brazil
*** Häggeboholm, Häggesled, S-53194 Järpås, Sweden

ABSTRACT

Inundation forests in Central Amazonia are covered by several metres of floodwater for 5-7 months each year, due to the monomodal flood pulse of rivers. Terrestrial invertebrates have adapted to this ecosystem by evolving several survival strategies. The Symphyla of a mixedwater inundation forest near Manaus comprised solely terricolous species, which represented non-migrants and migrants. Migratory reaction of *Hanseniella arborea* Scheller, 1979 was vertical, with temporal ascent of adults into tree trunks. The non-migrating species *Symphylella adisi* Scheller, 1992 and *Ribautiella amazonica* Scheller, 1984 had dormant stages under water. Subadults and advanced juvenile stages of *R. amazonica* spent the inundation period in naturally available retreats (inside tree roots). During the non-inundation period, abundance of this species was highest (52.6%) when compared to *H. arborea* (39.4%) and *S. adisi* (7.9%) of the total catch (n = 2139 specimens). Vertical distribution of all species in the soil (0-14 cm depth), their life cycle and the vertical migration of *H. arborea* are discussed with respect to abiotic factors in the study area.

RÉSUMÉ

Abondance, phénologie et histoire naturelle des symphyles d'une forêt inondable en Amazonie Centrale, Brésil.

Les forêts inondables de l'Amazonie Centrale sont couvertes par plusieurs mètres d'eau durant 5 à 7 mois de l'année, à cause de la fréquence d'inondations monomodales des rivières. Les invertébrés terrestres se sont adaptés à ce type particulier d'écosystème en faisant évoluer plusieurs stratégies de survie. Les symphyles d'une forêt inondable d'eau mixte près de Manaus comportent uniquement des espèces terricoles, représentées par des formes migratrices et non-migratrices. La migration de *Hanseniella arborea* Scheller, 1979 s'effectue verticalement, avec un déplacement temporaire d'adultes sur les troncs d'arbres. Les espèces non-migratrices *Symphylella adisi* Scheller, 1992 et *Ribautiella amazonica* Scheller, 1984 présentent, sous l'eau, des états de dormance. Les subadultes et les stades juvéniles avancés de *R. amazonica* passent la période d'inondation dans des retraites naturelles accessibles, notamment le système racinaire des arbres. En dehors de la période d'inondation, l'abondance de ces espèces est plus élevée (52,6%) que celles de *H. arborea* (39,4%) et de *S. adisi* (7,9%) par rapport au total des captures (n = 2139 individus). La répartition verticale de toutes les espèces dans le sol (0-14 cm de profondeur), leur cycle de vie et la migration verticale de *H. arborea* sont discutés par rapport aux facteurs abiotiques du site d'étude.

ADIS, J., DE MORAIS, J. W. & SCHELLER, U., 1996. — On abundance, phenology and natural history of Symphyla from a mixedwater inundation forest in Central Amazonia, Brazil. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 607-616. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

INTRODUCTION

Inundation forests in Central Amazonia and their adjacent shores are covered by several metres of floodwater for 5-7 months each year due to the monomodal periodic flood pulse of rivers (cf. JUNK *et al.*, 1989). Terrestrial invertebrates have adapted to this ecosystem by evolving several "survival strategies" (cf. ADIS, 1992a). The fauna comprises both terricolous and arboricolous animals. Both groups include non-migrants and migrants. Migratory reaction of terricolous animals is horizontal (following the high water line), vertical (temporal ascent to trunk or canopy) or includes a temporal flight to upland forests. Non-migrants have active or dormant stages under water. The latter pass inundation in naturally available retreats, in self-made retreats or as eggs. Non-migrant arboricolous animals reproduce and live exclusively in the trunk and canopy region, whereas migrants include life stages that live on the ground as well. Characteristics and examples of species for each of these categories are given by ADIS (1992a, b). In this paper, adaptive reaction of Symphyla from a mixed water inundation forest near Manaus to the annual flooding is discussed. Abundance, phenology and the natural history of three species are compared with data already known from symphylans inhabiting blackwater inundation forests in the Rio Negro valley (cf. ADIS & SCHELLER, 1984; SCHELLER & ADIS, 1984).

STUDY AREA AND METHODS

The study site was at Lago Janauarí (03°20'S, 60°17'W), situated on a spit between the Rio Negro and the Rio Solimões about 10 km from Manaus, across the river. The region was influenced by blackwater of the Rio Negro during low water-level and by whitewater of the Rio Solimões during the high water period. The study site in this seasonal mixed water inundation forest (cf. PRANCE, 1979) was flat and had no direct connection with non-flooded dryland (= upland) areas, which were several km distant (comp. Fig. 18 in IRMLER, 1975). The soil consisted of clay, predominantly montmorillonite, which represented alluvial deposits of the Rio Solimões. A scanty litter layer was formed during the non-inundation period (August/September - April/May). It was mostly carried out of the forest by the current of the annual floodwaters and/or partially covered by sediments deposited during inundation. Further information on the study site is given by ERWIN (1983), IRMLER (1975) and ADIS & RIGHI (1989).

Symphylans evaluated for this study were collected between June, 1987 and May, 1988. In 1987, inundation lasted until end of July. The study area was not flooded again until early May, 1988. On the forest floor, four ground photo-eclectors (= emergence traps) provided data on the activity density of symphylans. Ground photo-eclectors are round, tent-like capture devices which cover a basal area of 1 m^2. They consist of lateral plastic walls, a roof of black cloth, a transparent collecting box on top and a pitfall trap inside the apparatus. Trunk ascents and descents were detected at bi-weekly intervals with arboreal photo-eclectors (= funnel traps) on one tree trunk each throughout the collecting period. The traps consisted of four connected capturing funnels of black cloth, each with a transparent collecting box at the funnel mouth, and formed a closed ring around the trunk. The funnel opening faced either the forest floor (for trunk ascending animals) or the canopy (for trunk descending animals). Traps for trunk ascents were mounted on *Virola surinamensis* (ROL.) WARB. (Myristiaceae) and traps for trunk descents on *Hevea spruceana* MÜLL. ARG. (Euphorbiaceae), two dominant tree species in the study area. The killing/preserving agent used in all photo-eclectors on soil and trunk was aqueous picric acid solution (without detergent), which is known to be mostly neutral in terms of attraction or repellence in temperate zones (ADIS, 1979). In one of the four ground photo-eclectors, however, an aqueous formaldehyde solution (3%) was utilized. All capture devices are fully described by ADIS (1981) and FUNKE (1971) who also explain their mode of utilization and function. In addition, the distribution of symphylans in the soil was studied between August, 1987 and May, 1988 (non-inundation period). Once a month (cf. Figs 4, 8, 12) six soil samples were taken at random along a transect with a split corer (= steel cylinder with lateral hinges; diameter 21 cm, length 33 cm), which was driven into the soil by a mallet. Each sample of 14 cm was then divided into four subsamples of 3.5 cm each. Animals were extracted from subsamples following a modified method of KEMPSON (ADIS, 1987). In addition, symphylans were obtained from soil samples which were taken under water in August 1988 (end of flood period) as described above and subsequently extracted by means of a flotation method via sugar water (for methodology see ADIS *et al.*, 1989).

Seasonal inundation forests in Central Amazonia are subject to a rainy season (December - May: average precipitation 1550 mm), and a "dry" season (June - November: average precipitation 550 mm, but each month has some rain events; cf. RIBEIRO & ADIS, 1984). Vertical distribution of Symphyla in relation to changing conditions of soil moisture content, temperature and pH was statistically evaluated with the linear correlation test (CAVALLI-SFORZA, 1972), using the original field data. This method was also used to evaluate the activity of Symphyla on the soil surface and tree trunks in relation to insolation, precipitation, temperature and humidity of the air. The taxonomic work for this paper was done by U. SCHELLER (cf. SCHELLER, 1979, 1992; SCHELLER & ADIS, 1984), the collection and the evaluation of

Source : MNHN, Paris

field data by J. ADIS and J. W. DE MORAIS. Symphylans sampled were classified as juveniles (8, 9 and 10 pairs of legs), subadults (11 pairs of legs) and adults (12 pairs of legs). For subadults and adults sex was determined according to CHARDARD (1947) and SCHELLER (1979).

RESULTS AND DISCUSSION

A total of 2386 Symphyla were collected in the seasonal mixedwater inundation forest under study. Out of these, 97% could be classified to species and developmental stages. The majority were juveniles (48% of the total catch; n = 1105), 39% were adults (n = 899) and 13% subadults (n = 312). They comprised three species: *Ribautiella amazonica* Scheller, 1984 and *Symphylella adisi* Scheller, 1992 (Scolopendrellidae) were found solely in the soil (by soil extraction). *Hanseniella arborea* Scheller, 1979 (Scutigerellidae) was caught on the soil surface (in ground photo-eclectors) and also during trunk ascents and descents (in arboreal photo-eclectors).

During the non-inundation period, 79% of all symphylans obtained by soil extraction from the 0-14 cm cores were caught in the top 7 cm, irrespective of their developmental stage (cf. Fig. 1). Abundance of *R. amazonica* was highest (53%; 542 ind. m^{-2} $month^{-1}$), when compared to *H. arborea* (39%: 406 ind. m^{-2} $month^{-1}$) and *S. adisi* (8% of the total catch; 82 ind. m^{-2} $month^{-1}$). The highest population density, of 1853 ind. m^{-2}, was recorded during the dry season (in October, 1987) and the lowest, of 260 ind. m^{-2}, at the beginning of the non-inundation period (in August, 1987). Average abundance of Symphyla in the soil of the seasonal mixedwater forest (1766 ind. m^{-2} $month^{-1}$) was about nine times higher than the average from a seasonal blackwater inundation forest (208 ind. m^{-2} $month^{-1}$; ADIS & SCHELLER, 1984; SCHELLER & ADIS, 1984).

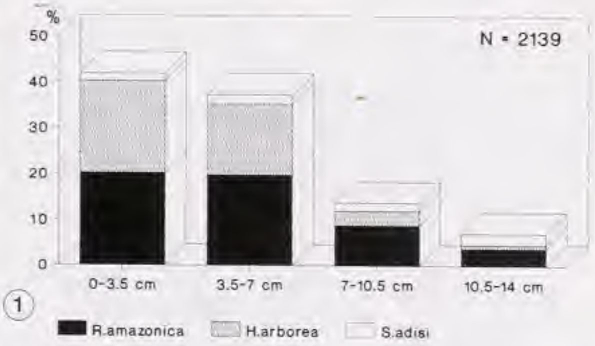


FIG. 1. — Distribution of Symphyla species in the soil. Monthly samples taken every 3.5 cm to a depth of 14 cm between August, 1987 and April, 1988 (non-inundation period) in a seasonal mixedwater inundation forest at Lago Janauarí; total catch = 100%.

Data from this study provided conclusive information on the life cycle, habitat and ecology of the three Symphyla species found.

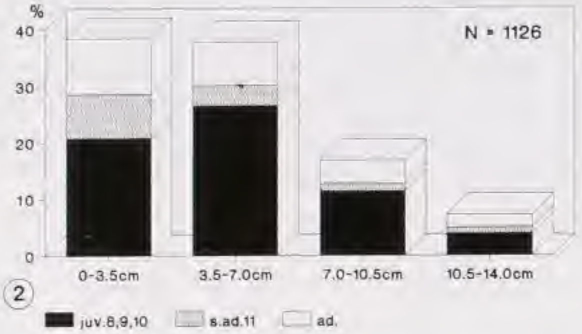
Ribautiella amazonica Scheller (Scolopendrellidae)

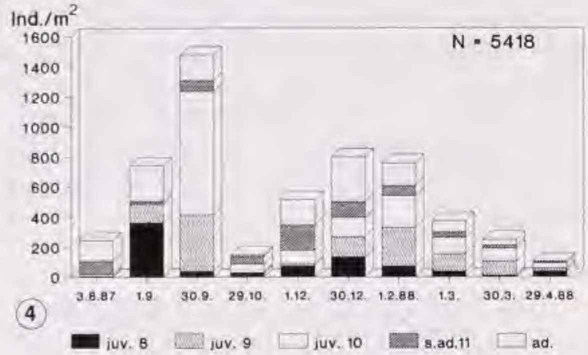
This terricolous non-migrating and univoltine species reaches 2.1 mm in length. It is known to pass inundation in the soil of seasonal blackwater inundation forests inside tree roots in a dormant state (ADIS, 1992b). This behaviour was reconfirmed for *R. amazonica* from the seasonal mixedwater forest, where subadults and the last juvenile stage (10 pairs of legs) were obtained by flotation of soil samples which were taken under water during forest inundation. Shortly after the floodwater had receded from the forest (in 1987 at the end of July), these symphylans had moulted to subadults and adults (Fig. 4).

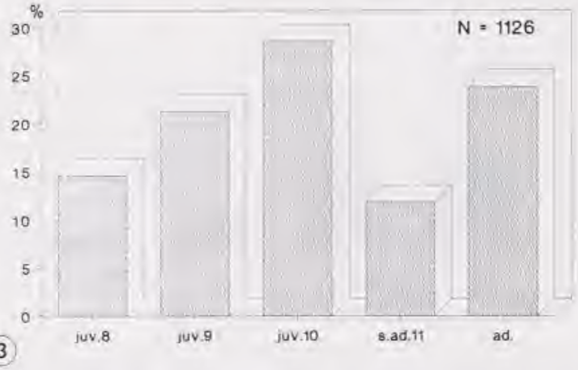
Soil extraction data, indicated that reproduction took place in the early part of the non-inundation period, as first juveniles of the offspring occurred from September onwards, four weeks after the forest floor had dried. *R. amazonica* is considered hemiedaphic, as 76% of all specimens extracted from soil samples in 1987/88 were found in the top 7 cm, irrespective of their developmental stage (Fig. 2). This is in contrast to data obtained from the seasonal

Source : MNHN, Paris

blackwater forest, where the species was considered euedaphic, as 86% of all specimens occurred below 7 cm soil depth (ADIS, 1992b).







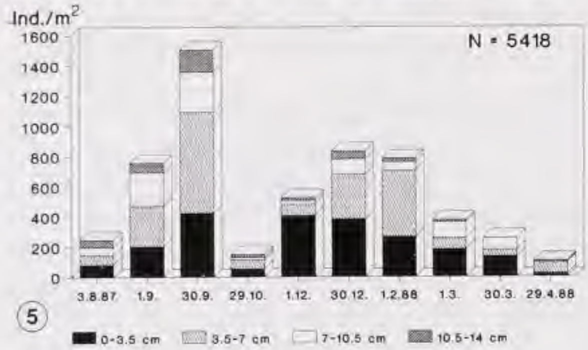


FIG. 2. — *Ribautiella amazonica* Scheller (Scolopendrellidae): Distribution of developmental stages in the soil at Lago Janauarí. Monthly samples taken every 3.5 cm to a depth of 14 cm between August, 1987 and April, 1988 (non-inundation period); total catch = 100%.

FIG. 3. — *Ribautiella amazonica* Scheller (Scolopendrellidae): Percentage of developmental stages caught in the soil (0-14 cm depth). Monthly samples taken between August, 1987 and April, 1988 (non-inundation period) at Lago Janauarí.

FIG. 4. — *Ribautiella amazonica* Scheller (Scolopendrellidae): Temporal occurrence and abundance of developmental stages (ind./m2) in the soil (0-14 cm depth). Monthly samples taken between August, 1987 and April, 1988 (non-inundation period) at Lago Janauarí.

FIG. 5. — *Ribautiella amazonica* Scheller (Scolopendrellidae): Temporal occurrence and abundance (ind./m2) of specimens in the soil at Lago Janauarí. Monthly samples taken every 3.5 cm to a depth of 14 cm between August, 1987 and April, 1988 (non-inundation period).

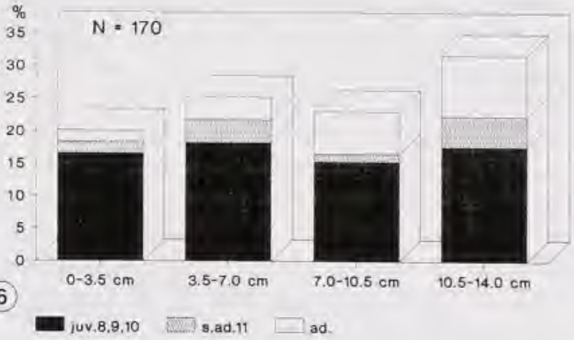
About 64% of the *Ribautiella* population in the seasonal mixedwater forest was represented by juveniles (Fig. 3), 12% by subadults and 24% by adults. The sex ratio of males and females was 1: 1.2 (n = 268). Population density was lowest two weeks prior to inundation (April 29, 1988: 250 ind. m-2), when most of the symphylans must have entered tree roots to pass flooding in a dormant state. Abundance was highest eight weeks after inundation had ended (September 30, 1987: 1,477 ind. m-2), due to a high number of juveniles of the progeny in the upper 7 cm of the soil (Figs 4, 5).

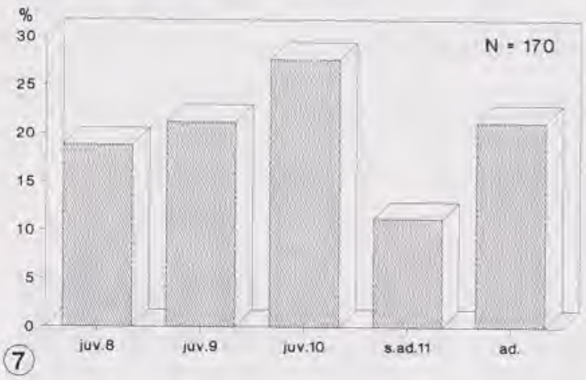
There was no clear correlation between the vertical distribution of *R. amazonica* in the soil throughout the non-inundation period and the abiotic factors monitored in the study area.

Source : MNHN, Paris

Symphylella adisi Scheller (Scolopendrellidae)

This is the smallest of the three species collected in the seasonal mixedwater inundation forest reaching a maximum of 1.5 mm in length. It was only found in the soil but was recorded from all soil layers sampled (Figs 6, 9). About 68% of its population was represented by juveniles, 11% by subadults and 21% by adults (Fig. 7). The sex ratio of males and females was 1: 1.1 (n = 35). The population density was lowest two weeks prior to forest inundation (April 29, 1988: 5 ind. m^{-2}) and highest during the early rainy season (February 2, 1988: 327 ind. m^{-2}). There was no correlation found between the population density of *S. adisi* and weather conditions in the area (dry season versus rainy season).





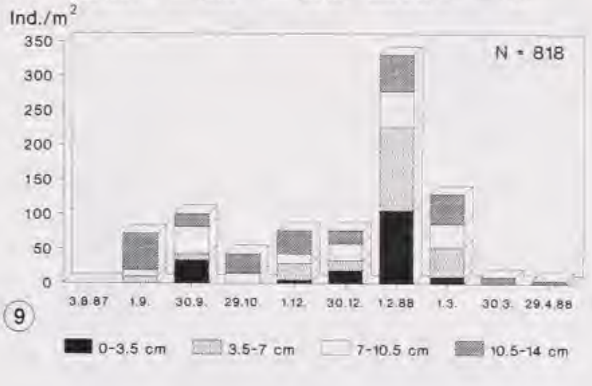


FIG. 6. — *Symphylella adisi* Scheller (Scolopendrellidae): Distribution of developmental stages in the soil at Lago Janauarí. Monthly samples taken every 3.5 cm to a depth of 14 cm between August, 1987 and April, 1988 (non-inundation period); total catch = 100%.

FIG. 7. —*Symphylella adisi* Scheller (Scolopendrellidae): Percentage of developmental stages caught in the soil (0-14 cm depth). Monthly samples taken between August, 1987 and April, 1988 (non-inundation period) at Lago Janauarí.

FIG. 8. — *Symphylella adisi* Scheller (Scolopendrellidae): Temporal occurrence and abundance of developmental stages (ind./m^2) in the soil (0-14 cm depth). Monthly samples taken between August, 1987 and April, 1988 (non-inundation period) at Lago Janauarí.

FIG. 9. — *Symphylella adisi* Scheller (Scolopendrellidae): Temporal occurrence and abundance (ind./m^2) of specimens in the soil at Lago Janauarí. Monthly samples taken every 3.5 cm to a depth of 14 cm between August, 1987 and April, 1988 (non-inundation period).

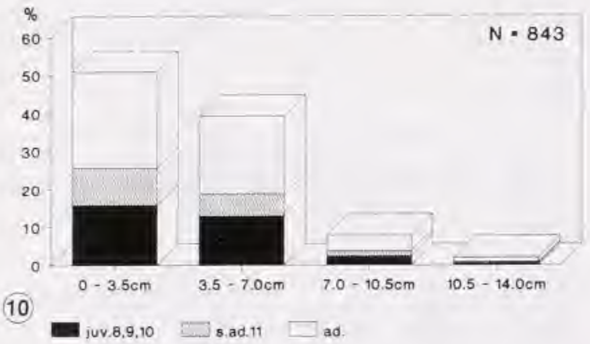
It is presumed, that *S. adisi* passed forest inundation in a dormant state in the soil. Due to its low abundance, it has not yet been located in soil samples taken under water during the flood period and the type of its retreat (naturally available or self-made) is still unknown. Six weeks after the forest floor had dried, adults and early juvenile stages of their offspring (8 and 9 pairs

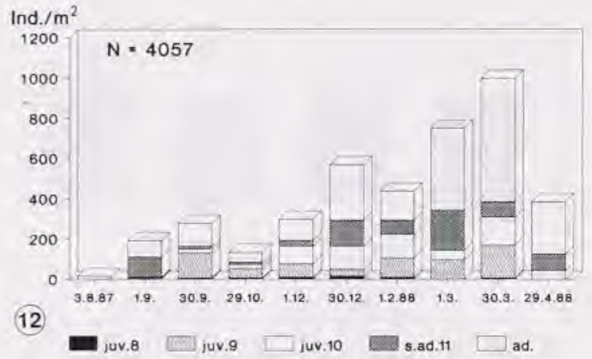
Source : MNHN, Paris

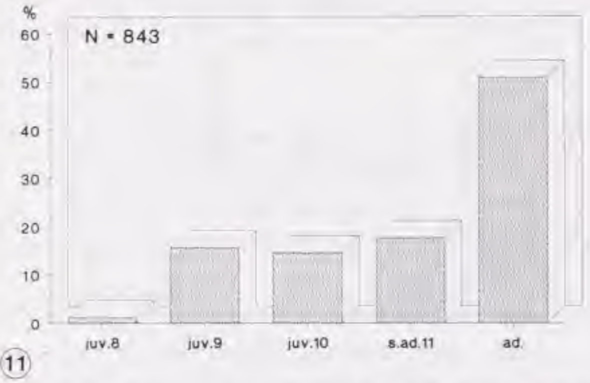
of legs) were found in 3.5 - 14 cm soil depth (Figs 8, 9). Subadults occurred from end of October onwards. The highest number of juvenile stages was observed during the early rainy season (in February; Fig. 8) and main reproduction is assumed to occur at this time. The abundance of subadults subsequently declined and advanced juvenile stages (9 and 10 pairs of legs) as well as subadults dominated (Fig. 8). Ten weeks prior to inundation, only a few specimens were found and those solely in the lowest of the soil layers sampled (10.5 - 14 cm; Fig. 9). The main part of the population most probably had entered retreats at this time and, due to the dormant state, could not be obtained by means of the soil extraction method.

Based on the characteristics outlined, *S. adisi* is considered a terricolous non-migrating and univoltine species with dormant stages (presumably of subadults and advanced juveniles) in retreats under water during annual inundation.

Hanseniella arborea Scheller (Scutigerellidae)







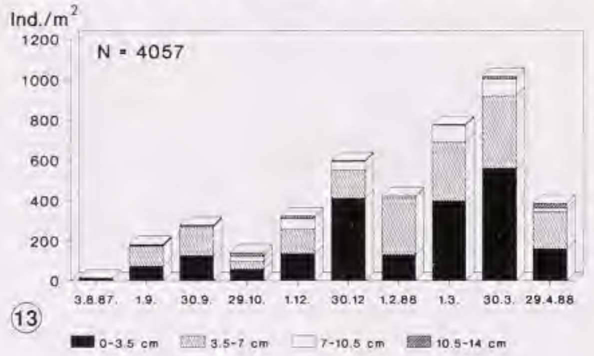


FIG. 10. — *Hanseniella arborea* Scheller (Scutigerellidae): Distribution of developmental stages in the soil at Lago Janauarí. Monthly samples taken every 3.5 cm to a depth of 14 cm between August, 1987 and April, 1988 (non-inundation period); total catch = 100%.

FIG. 11. — *Hanseniella arborea* Scheller (Scutigerellidae): Percentage of developmental stages caught in the soil (0-14 cm depth). Monthly samples taken between August, 1987 and April, 1988 (non-inundation period) at Lago Janauarí.

FIG. 12. — *Hanseniella arborea* Scheller (Scutigerellidae): Temporal occurrence and abundance of developmental stages (ind./m^2) in the soil (0-14 cm depth). Monthly samples taken between August, 1987 and April, 1988 (non-inundation period) at Lago Janauarí.

FIG. 13. — *Hanseniella arborea* Scheller (Scutigerellidae): Temporal occurrence and abundance (ind./m^2) of specimens in the soil at Lago Janauarí. Monthly samples taken every 3.5 cm to a depth of 14 cm between August, 1987 and April, 1988 (non-inundation period).

This terricolous, migrating and univoltine species reaches 2.7 mm in length. Adults are known to pass inundation in the trunk/canopy area of seasonal blackwater inundation forests

Source : MNHN, Paris

(ADIS & SCHELLER, 1984). This behaviour was reconfirmed for *H. arborea* from the seasonal mixedwater inundation forest (Fig. 14).

In the soil, about 51% of the population caught during the non-inundation period was represented by adults (the migrating stage), 31% by juveniles and 18% by subadults. The sex ratio of males and females was 1 : 1.5 (n = 429). *H. arborea* is considered hemiedaphic, as 51% of all specimens extracted from soil samples in 1987/88 were found in the top 3.5 cm and 90% in 0-7 cm soil depth, irrespective of their developmental stage (Figs 10, 13). Data differs somewhat from results obtained in the seasonal blackwater forest, where *H. arborea* was most abundant in 3.5 - 7 cm soil depth (47% of the total catch), and where only 12% of all specimens were obtained from the top 3.5 cm (ADIS & SCHELLER, 1984). First analysis of grain size and mineral composition of soils from mixed- and blackwater inundation forests (ADIS & IRION, unpubl.) indicated, that a lower abundance of *H. arborea* in the soil layers sampled corresponded with a greater presence of grains < 2 µm, due to a higher amount of clay. In the seasonal mixedwater forest under study, decrease in population density of *H. arborea* from the top 3.5 cm to 14 cm soil depth (cf. Fig. 10) was correlated with an increase of grains < 2 µm and of clay from 32% to 49% per soil layer ($p < 0.10$ for the total catch, $p < 0.05$ for monthly catches of Oct.10 and Dec. 12, 1987 & March 1 and 30, 1988). In the seasonal blackwater inundation forest, abundance of *H. arborea* was highest where the amount of grains < 2 µm and of clay was the lowest (12% in 3.5 - 7 cm soil depth) as compared to the soil layers below (25 - 31% in 7-14 cm depth), where abundance was lower (cf. Fig. 3 *in* ADIS & SCHELLER, 1984).

It is suggested, that *H. arborea* might have difficulties inhabiting fine and clayey soil layers due to its relatively large size.

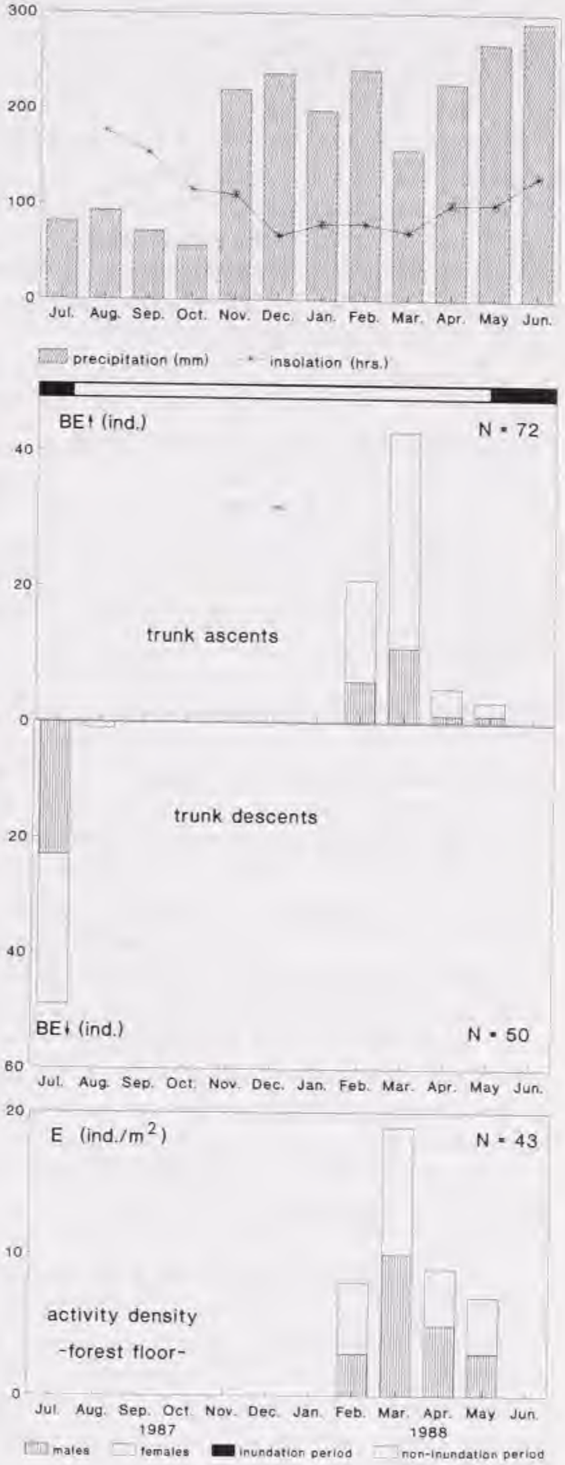


FIG. 14. — *Hanseniella arborea* Scheller (Scutigerellidae): Activity density of males and females on the forest floor (4 ground photo-eclectors: (E); ind./m²), trunk descents (BE ↓) and trunk ascents (BE ↑); one arboreal photo-eclector, respectively) between July, 1987 and June, 1988 at Lago Janauarí.

Source : MNHN, Paris

The lowest abundance of this species in soils from the mixedwater area was observed during the beginning of the non-inundation period (August 3, 1987: 14 ind. m^{-2}). *H. arborea* was at this time represented by adults which had returned from the trunk/canopy area after flooding and recolonized the upper 3.5 cm of the forest floor (Figs 12-14). Juvenile stages and subadults of the progeny were detected only four weeks later (Fig. 12). Their abundance was highest during the beginning of the rainy season (in December/January), shortly after the main reproduction must have occurred. Adults dominated between February and April (Fig. 12) when they came to the surface (where they were caught in ground photo-eclectors) and started ascending tree trunks, about 12 weeks prior to forest inundation (Fig. 14). The predominance of females assured the continuation of this species. During periods of less insolation, the number of adults caught in arboreal photo-eclectors was lower ($p < 0.05$). No significant correlation was found between catch numbers and the increasing water-level of the Rio Negro (cf. ADIS *et al.*, this volume). In the seasonal blackwater inundation forest, adults of *H. arborea* occurred more frequently in ground photo-eclectors after heavy rainfalls, compared to drier periods ($p < 0.05$; cf. ADIS & SCHELLER, 1984).

Phenology data of *H. arborea* from this mixedwater study area supports the life cycle proposed for this species based on results obtained by ADIS & SCHELLER (1984) from the seasonal blackwater inundation forest.

CONCLUSIONS

Four terricolous species of Symphyla were found to inhabit the soils of different non-flooded upland forests in Central Amazonia: *Scolopendrellopsis tropicus*, *Symphylella adisi*, *Ribautiella amazonica* (Scolopendrellidae), and *Hanseniella arborea* (Scutigerellidae; cf. SCHELLER, 1992).

Results of this paper show, that three of them succeeded in colonizing seasonally inundated forests of the mixedwater and blackwater type in the Rio Negro valley. The survival strategies which have evolved include a migratory state, represented by adults which pass inundation in the trunk/canopy area (Scutigerellidae) and a dormant state, represented by advanced juvenile and subadult stages which pass the flood period under water in retreats (Scolopendrellidae). The concentration of dissolved oxygen in the water body near the soil is known to be so low that flood resistant symphylans may have to switch from plastron and cutaneous respiration to anaerobic respiration (ADIS & MESSNER, 1991; MESSNER & ADIS, 1988, 1992). The first and second larval stages (6 and 7 pairs of legs respectively) of the three symphylan species may be inactive (TIEGS, 1945) or may only last a short time, as they were not obtained by means of the soil extraction method. Only the migrating species *H. arborea* was observed to respond to abiotic changes in its environment. Activity density on the soil surface and vertical migration were somewhat triggered by these secondary ecofactors which are no longer directly related to the cycle of flooding, and to which many terrestrial invertebrates of inundation forests have become sensitive (cf. ADIS, 1992a). The flood pulse (JUNK *et al.*, 1989) is regarded as the original determinant of trunk ascents and descents. However, it was found to act as the primary control mechanism or ecofactor among a few invertebrate species only (ADIS, 1992a).

Evaluation of capture data also indicated, that the three symphylan species changed from a plurivoltine mode of life in upland forests (ADIS, MORAIS, RODRIGUES & SCHELLER, unpubl.) to an univoltine life cycle in inundation forests. This was also observed in Pseudoscorpiones and Meinertellidae (Archaeognatha) from the same study areas (ADIS *et al.*, 1988; ADIS & STURM, 1987). It remains to be investigated if the species of Symphyla in inundation forests already differ ecologically and phenologically, as well as genetically, to such a great degree from those in upland forests that they must be regarded as new species or subspecies (cf. WOLF & ADIS, 1992).

Source : MNHN, Paris

ACKNOWLEDGEMENTS

We are indebted to all our colleagues at the National Institute of Amazonian Research (INPA) in Manaus (Brazil) and at the Max-Planck-Institute for Limnology in Plön (Germany) who, in the field or laboratory, contributed to this study, especially Susanne HAMANN, Irmgard ADIS, Edilson DE ARAUJO SILVA and M. Sc. Elizabeth FRANKLIN. Dr. Helen READ (Bucks, United Kingdom) kindly corrected the English manuscript. This study was supported by a grant from the German Academic Exchange Service (DAAD) for the second author and from the Max-Planck-Society for the third author. We wish to acknowledge the valuable support received by PD Dr. W. J. JUNK, head of the Tropical Ecology Working Group at the Max-Planck-Institute for Limnology in Plön, Germany.

REFERENCES

ADIS, J., 1979. — Problems of interpreting arthropod sampling with pitfall traps. *Zool. Anz.*, **202** : 177-184.

ADIS, J., 1981. — Comparative ecological studies of the terrestrial arthropod fauna in Central Amazonian inundation forests. *Amazoniana*, **7** : 87-173.

ADIS, J., 1987. — Extraction of arthropods from Neotropical soils with a modified KEMPSON apparatus. *J. Trop. Ecol.*, **3** : 131-138.

ADIS, J., 1992a. — Überlebensstrategien terrestrischer Invertebraten in Überschwemmungswäldern Zentralamazoniens. *Verh. naturwiss. Ver. Hamburg*, **33** : 21-114.

ADIS, J., 1992b. — How to survive six months in a flooded soil: Strategies in Chilopoda and Symphyla from Central Amazonian floodplains. *In*: : J. ADIS & S. TANAKA, *Symposium on life-history traits in tropical invertebrates*. [INTECOL, Yokohama, Japan 1990. *Studies on Neotropical Fauna and Environment*, **27**], Lisse, Swets & Zeitlinger : 117-129

ADIS, J., MAHNERT, V., MORAIS, J. W. DE & RODRIGUES, J. M. G., 1988. — Adaptation of an Amazonian pseudoscorpion (Arachnida) from dryland forests to inundation forests. *Ecology*, **69** : 287-291.

ADIS, J. & MESSNER, B., 1991. — Langzeit-Überflutungsresistenz als Überlebensstrategie bei terrestrischen Arthropoden. - Beispiele aus zentralamazonischen Überschwemmungsgebieten. *Dtsch. ent. Z., N. F.*, **38** : 211-223.

ADIS, J., MESSNER, B. & GROTH, I., 1989. — Zur Überflutungsresistenz und zum Spinnvermögen von Japygiden (Diplura). *Zool. Jb. Anat.*, **119** : 371-382.

ADIS, J. & RIGHI, G., 1989. — Mass migration and life cycle adaptation - a survival strategy of terrestrial earthworms in Central Amazonian inundation forests. *Amazoniana*, **11** : 23-30.

ADIS, J. & SCHELLER, U., 1984. — On the natural history and ecology of *Hanseniella arborea* Scheller, (Myriapoda, Symphyla, Scutigerellidae), a migrating symphylan from an Amazonian black-water inundation forest. *Pedobiologia*, **27** : 35-41.

ADIS, J. & STURM, H., 1987. — On the natural history and ecology of Meinertellidae (Archaeognatha, Insecta) from dryland and inundation forests of Central Amazonia. *Amazoniana*, **10** : 197-218.

CAVALLI-SFORZA, L., 1972. — *Grundzüge biologisch-medizinischer Statistik*. Stuttgart, G. Fischer, 212 pp.

CHARDARD, R., 1947. — Nouvelles stations de Symphyles, distinction et rapport numérique des sexes. *Bull. Mus. Natl. Hist. nat. Paris*, (2), **19** : 177-184.

ERWIN, T. L., 1983. — Beetles and other insects of tropical forest canopies at Manaus, Brazil, sampled by insecticidal fogging,. *In*: : S. L. SUTTON, T. C. WHITMORE & A. C. CHADWICK, *Tropical Rain Forest: Ecology and Management*. Oxford, Blackwell Scientific Publications : 59-75.

FUNKE, W., 1971. — Food and energy turnover of leaf-eating insects and their influence on primary production. *Ecological Studies*, **2** : 81-93.

IRMLER, U., 1975. — Ecological studies of the aquatic soil invertebrates in three inundation forests of Central Amazonia. *Amazoniana*, **5** : 337-409.

JUNK, W. J., BAYLEY, P. B. & SPARKS, R. E., 1989. — The flood pulse concept in river-floodplain systems. *Can. Spec. Publ. Fish. Aquat. Sci.*, **106** : 110-127.

MESSNER, B. & ADIS, J., 1988. — Die Plastronstrukturen der bisher einzigen submers lebenden Diplopodenart *Gonographis adisi* Hoffman 1985 (Pyrgodesmidae, Diplopoda). *Zool. Jb. Anat.*, **117** : 277-290.

MESSNER, B. & ADIS, J., 1992. — Die Plastronatmung bei aquatischen und flutresistenten terrestrischen Arthropoden (Acari, Diplopoda und Insecta). *Mitt. Dtsch. Ges. Allg. Angew. Ent.*, **8** : 325-327.

PRANCE, G. T., 1979. — Notes on the vegetation of Amazonia III. The terminology of Amazonian forest types subject to inundation. *Brittonia*, **31** : 26-38.

Source : MNHN, Paris

RIBEIRO, M. DE N. G. & ADIS, J., 1984. — Local rainfall variability - a potential bias for bioecological studies in the Central Amazon. *Acta Amazonica*, **14** : 159-174.

SCHELLER, U., 1979. — *Hanseniella arborea* n. sp., a migrating symphylan from an Amazonian blackwater inundation forest (Myriapoda, Symphyla, Scutigerellidae). *Acta Amazonica*, **9** : 603-607.

SCHELLER, U., 1992. — A study of neotropical Symphyla (Myriapoda): list of species, keys to genera and description of two new Amazonian species. *Amazoniana*, **12** : 169-180.

SCHELLER, U. & ADIS, J., 1984. — A new species of *Ribautiella* (Myriapoda, Symphyla, Scolopendrellidae) from an Amazonian black-water inundation forest and notes on its natural history and ecology. *Amazoniana*, **8** : 299-310.

TIEGS, O. W., 1945. — The post-embryonic development of *Hanseniella agilis* (Symphyla). *Quart. Jour. Micros. Sci.*, **85** : 192-328.

WOLF, H. G. & ADIS, J., 1992. — Genetic differentiation between populations of *Neomachilellus scandens* (Meinertellidae, Archaeognatha, Insecta) inhabiting neighbouring forests in Central Amazonia. *Verh. naturwiss. Ver. Hamburg*, **33** (NF) : 5-13.

Source : MNHN, Paris

The Ecology of Savanna Millipedes in Southern Africa

John Mark DANGERFIELD * & *Steven R. TELFORD* **

* Department of Biological Sciences, University of Botswana
PB 0022, Gaborone, Botswana
** Department of Zoology, University of Pretoria
Pretoria 0002, South Africa

ABSTRACT

Millipedes of the order Spirostreptida are abundant and diverse in the savanna habitats of southern Africa. Large body size (2-20g live mass), mobility and considerable local abundance of up to 30 individuals per square meter are features of several species. Life cycles and behaviours are strongly influenced by the seasonality of the climate whilst short term changes in atmospheric conditions induce bouts of conspicuous surface activity during summer. The cylindrical body plan is efficient for burrowing and enables individuals to find shelter in the soil during the dry winter. Energy efficient mobility allows for opportunistic foraging tactics within a generalist feeding strategy. These tactics can result in the development of high density aggregations on suitable food sources. Few species appear to be exclusively litter feeders although some species specialise on algae. Relatively low assimilation efficiencies require high ingestion rates and in some habitats the turnover of detrital material by millipedes may have a significant influence on nutrient cycling. Millipede species diversity, in particular relative abundance, varies between habitats and appears to be related to the composition and vertical expression of the vegetation. Millipede communities in savannas are likely to be input driven but biotic interactions, including interspecific competition, may also be important.

RÉSUMÉ

L'écologie des diplopodes de savanne en Afrique du Sud.

Les diplopodes de l'ordre Spirostreptida sont abondants et diversifiés dans les écosystèmes de savane d'Afrique du Sud. La grande taille du corps (2 à 20 g de masse fraîche), la mobilité et l'abondance considérable, dépassant localement 30 individus par mètre carré, caractérisent plusieurs espèces. Le cycle biologique et le comportement paraissent fortement influencés par l'aspect saisonnier du climat tandis que les changements à court terme des conditions atmosphériques induisent des reprises d'activité manifestes en surface durant l'été. La forme cylindrique du corps est efficace pour l'enfouissement et permet aux individus de trouver des abris dans le sol durant l'hiver sec. L'énergie allouée à la mobilité facilite les tactiques opportunistes de recherche de la nourriture au sein d'une stratégie alimentaire généraliste. Ces tactiques peuvent provoquer l'apparition d'une distribution fortement agrégative avec de fortes densités sur les sites de répartition des ressources alimentaires. Quelques espèces apparaissent comme des consommatrices exclusives de litière bien que quelques-unes se spécialisent dans la consommation des algues. Les rapports d'assimilation relativement bas requièrent des taux d'ingestion élevés et, dans certains milieux, le renouvellement des matériaux organiques fragmentés par les diplopodes peut avoir une influence significative sur le cycle des éléments minéraux. La diversité spécifique des diplopodes, notamment l'abondance relative des espèces, varie selon les milieux et semble être reliée à la composition et à la répartition verticale de la végétation. Il semble que l'organisation des peuplements de diplopodes des savanes soit largement déterminée par les apports énergétiques mais les interactions biotiques, incluant notamment la compétition interspécifique, peuvent jouer aussi un rôle important dans l'élaboration de ces communautés d'arthropodes.

DANGERFIELD, J. M.,& TELFORD, S. R., 1996. — The ecology of savanna millipedes in Southern Africa. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 617-625. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

INTRODUCTION

In southern Africa the savanna environment covers a large area north of the tropic of Capricorn. A wide range of habitats occur characterized by a drought resistant vegetation mixture in which C_4 grasses potentially dominate the ground layer and woody plants vary in density from widely scattered individuals to a closed canopy woodland broken occasionally by drainage line grasslands (HUNTLEY, 1982). The functioning of these systems is driven primarily by the availability of water which is supplied seasonally in summer rainfall (October-April), although rainfall pattern and intensity are spatially and temporally unpredictable in volume and intensity (VOSSEN, 1988). Also characteristic is a dry and cool winter season. The severity and frequency of fires (TROLLOPE, 1982), soil nutrient status (SCHOLES, 1990) and a wide range of secondary factors influence the vegetation structure which varies on a number of spatial scales from 100's km in response to rainfall gradients through 10's km in response to soil type and geomorphology down to 10's m due to localised disturbance and nutrient enrichment by termites (CAMPBELL *et al*, 1988).

Although millipedes are abundant and diverse in these habitats (LAWRENCE, 1984; DANGERFIELD & TELFORD, 1992) their ecology is poorly known. Savanna ecosystems present ecological conditions for detritivores that place a premium on 1) avoidance of moisture stress, particularly desiccation, 2) resource acquisition and 3) the ability to withstand unpredictable stress including temporary food shortages.

Hence, in this paper we summarise our work on savanna millipedes in relation to the evolutionary pressures created by this type of environment. We also consider the influence of millipedes on the nutrient dynamics of savannas.

STUDY SITES

Much of the current study was carried out on three contrasting sites: 1) heterogeneous miombo woodland at Marondera, Zimbabwe, dominated by the canopy trees *Brachystegia spiciformis* and *Julbernardia globiflora* described in detail by CAMPBELL *et al* (1988); 2) *Acacia* savanna in south-east Botswana dominated by *Acacia erubescens*, *Dichrostachys cinerea*, and *Euclea undulata* (DANGERFIELD, MILNER & MATTHEWS, 1993) and 3) riparian savanna in south-east Botswana dominated by *Combretum erythrophyllum* (DANGERFIELD & MILNER, in press). A number of additional sites were studied including managed areas derived from miombo woodland (arable fields, pasture and plantations) and natural savanna types in Zimbabwe (riparian dominated by *Celtis africana*, *Burkea africana* woodland and *Colophospermum mopane* woodland) and Botswana (*Baikiaea plurijunga* woodland, *C. mopane* woodland and suburban habitats).

COMPOSITION AND ABUNDANCE OF THE MILLIPEDE FAUNA

Approximately 350 millipede species are thought to occur in southern Africa (LAWRENCE, 1984). The majority in savannas are juliform species of the order Spirostreptida, in particular members of the Spirostreptidae, Odontopygidae and Harpagophoridae approximately in the ratio of 2:1:1. Occasionally polydesmids, a group common in west Africa (LEWIS, 1971) and India (BHAKAT, 1989), can be found in the more moist habitats (>1000 mm rainfall) or synanthropic sites.

Many of the southern African spirostreptids are characterised by large body size, frequently in excess of 2.0 g fresh mass and in some species, such as *Alloporus uncinatus* (Attems), up to 20.0 g. Although LAWRENCE (1984) considers that these animals have localised distributions we have found several species over wide geographic areas. *A. uncinatus* is common from Zululand to north-east Zimbabwe and across to southern Botswana, an area of more than 10,000 km^2, similarly separate populations of *Calostreptus carinatus* have been recorded throughout this zone. However, along with the taxonomy (R. L. HOFFMAN, pers. comm.), the biogeography of these species remains poorly known.

The abundance of millipedes in savannas varies greatly between the habitat types (Table 1) and, together with other soil animals, many species appear to be sensitive to habitat change,

Source : MNHN, Paris

particularly when natural habitats are converted for human land use (DANGERFIELD, 1990). In favourable sites total millipede densities can reach 30 Ind. m^{-2}, although accurate estimates of abundance are difficult to obtain because some species remain cryptic even during the rainy season, hence more than one sampling method is required for accurate estimates of abundance and small-scale distribution appears to be highly aggregated. The range in abundance of <1 to 35 Ind. m^{-2} is similar to that observed for other tropical species (BANERJEE, 1980; BHAKAT, 1989) but rather less than the 800 Ind. m^{-2} recorded for *Jonespeltis splendidus* (Verhoeff) (BANO & KRISHNAMOORTHY, 1985).

TABLE 1. — Abundance estimates (individuals $m^{-2} \pm 1$ standard error) for millipede assemblages in southern African grass and woodland savannas. Data sources: 1) DANGERFIELD (1990); 2) DANGERFIELD, MILNER & MATTHEWS (1993); 3) DANGERFIELD & MILNER (in press), 4) DANGERFIELD (unpublished data) and 5) DANGERFIELD & TELFORD (1993).

Habitat	Abundance	Sampling method
Miombo woodland	26 ± 5	soil monoliths[1]
Acacia savanna	0.4	visual inspection of permanent quadrats[2]
Riparian savanna	12 ± 3	litter quadrats ($1 m^2$)[3]
Teak woodland (*Baikiaea plurijunga*)	2 ± 1	soil monoliths[4]
Riparian savanna (*Acacia erioloba*)	25 ± 5	soil monoliths[4]
Mixed riparian	22 ± 5	soil monoliths[4]
Mopane (*Colophospermum mopane*)	33 ± 5	soil monoliths[4]
Plantation (*Pinus patula*)	0.3	visual inspection of permanent quadrats[5]

SURFACE ACTIVITY

Most adult spirostreptids, odontopygids and harpagophorids show distinct patterns of surface activity during the summer rainfall season from October to April (DANGERFIELD & TELFORD, 1991; DANGERFIELD, MILNER & MATTHEWS, 1993). During such activity individuals are conspicuous on the surface or can be located beneath leaf litter at the soil litter interface. Frequently individuals climb trees, shrubs and tall grasses. This behaviour may be to avoid waterlogged conditions, particularly in riparian habitats with clay rich soils; to access additional food sources such as microbial populations; or to avoid mates (see TELFORD & DANGERFIELD, this volume). *A. uncinatus*, *Chaleponcus limbatus* and *C. digitatus* can be added to two other southern African pill millipedes, *Sphaerotherium cinctellum* and *S. punctulatum*, that have been observed climbing trees (HAACKER & FUCHS, 1972).

The onset of surface activity appears to be initiated by the second major rainfall event (>20 mm) of the season as few animals are seen active after the first rainfall. Significant rainfall may be necessary for moisture to percolate the desiccated upper soil horizons to depths of up to 30 cm, where the animals overwinter, and break aestivation. An alternative hypothesis is that

Source : MNHN, Paris

delayed emergence may avoid late dry season fires which are a common feature of savannas. Not all species emerge at the same time. In *Acacia* savanna *Calostreptus carinatus*, which feeds primarily on algae, emerges four to five weeks after the first *A. uncinatus* and *Chaleponcus digitatus* are recorded which suggests that food availability may also influence emergence pattern.

There are considerable species specific differences in activity patterns within the rainfall season, and between site differences in overall millipede activity. In miombo woodland surface activity, measured as relative abundance, peaks in early December and then declines steadily (DANGERFIELD & TELFORD, 1991) whilst in wetter riparian habitats the early season peak occurs but the activity decline is less pronounced (TELFORD & DANGERFIELD, 1993). In the semi-arid *Acacia* savanna of south-east Botswana where rainfall is more sporadic millipede activity is pulsed, initially in response to each rainfall event but during February and March substantial rainfall events fail to produce significant millipede activity (DANGERFIELD, MILNER & MATTHEWS, 1993). REDDY & VENKATAIAH (1990) also found positive correlations between millipede abundance in pitfall traps and rainfall and soil moisture in both grass and tree savanna in India.

During surface activity individuals of all species were observed walking, feeding, resting, burrowing or copulating. The frequency with which these activities were observed varied between species and with sex (DANGERFIELD, MILNER & MATTHEWS, 1993; DANGERFIELD & KAUNDA, 1994). Seasonal variation in the proportion of observations of these behaviours in *Acacia* savanna is illustrated in Figure 1. *Alloporus uncinatus* was most frequently observed moving around the habitat and mobility appeared to increase through the season at the expense of feeding. In *Chaleponcus digitatus* feeding and walking were equally important and there was a higher frequency of individuals resting. *Calostreptus carinatus* also increased mobility during the season to the extent that in February and March no individuals were seen resting.

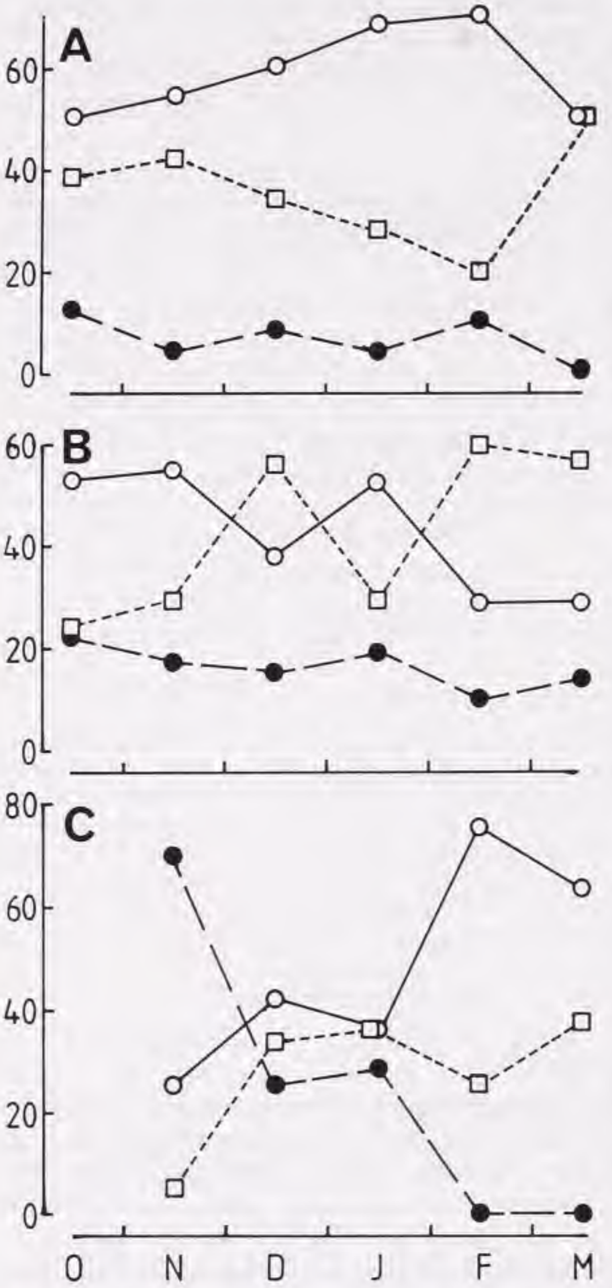


FIG.1. — Percentage of total observations (ordinate %) in three categories; walking (○—○), feeding (□—□) and resting (●—●) for *Alloporus uncinatus* (A), *Chaleponcus digitatus* (B) and *Calostreptus carinatus* (C) during the 1991-92 rainfall season in *Acacia* savanna, south-east Botswana.

Source : MNHN, Paris

FEEDING BEHAVIOUR

In field observations of behaviour during surface activity up to 52% of all records were of individuals feeding. A wide range of food sources were utilized including, tree leaf litter, seeds, grass litter, *Aloe grandidentata* litter, soil, algae, faeces and dead invertebrates which confirms for savanna species the wide dietary range seen in other diplopods (COLE, 1946; LEWIS, 1971; WOOTON & CRAWFORD, 1975; POBOZSNY, 1986 & review by CRAWFORD, 1992). A feature of these food types is that they represent a range of quality in terms of both energy and nutrient content from relatively poor quality grass litter, known to retard growth and reproductive output in woodlice (RUSHTON & HASSALL, 1983), to the nutrient rich cotyledons of *Acacia* seeds. Given such a range of foods energetic returns will vary with both the choice and quantity of material ingested.

In a series of laboratory experiments a number of species were fed partially ground *Combretum erythrophyllum* leaf litter and gravimetric estimates of ingestion and assimilation recorded (DANGERFIELD & MILNER, 1993). Individuals ingested between 2.6 and 7.6% of their dry body mass each day and assimilated around 10 to 25% of this material (Table 2), results that are consistent with those recorded for other millipede species (see references in DANGERFIELD & MILNER, 1993). The discrepancy between ingestion and assimilation is considerable. Variation in ingestion explains only 35 to 53% of variation in assimilation. The proportion of soil in the diet influences assimilation rates in *A. uncinatus* (DANGERFIELD, 1993), whilst available moisture, temperature, barometric pressure and food quality may also be important. There is much to be gained from experiments designed to consider the fitness consequences of specialist and catholic diets in detritivores.

TABLE 2. — Mean body size (mg dry mass) and estimates of mean (± 1 s.e.) ingestion rate (I, mg day-1), assimilation rate (A, mg day-1) and assimilation efficiency (AE, %) for five species of savanna millipede fed ground *Combretum erythrophyllum* litter. Data source: DANGERFIELD & MILNER (1993).

Family/Species	mean body mass	I	A	AE
Spirostreptidae				
Alloporus uncinatus	2.86 ± 0.14	75 ± 7	1.5 ± 2.9	18 ± 3
Calostreptus carinatus	0.22 ± 0.03	17 ± 2	4.3 ± 1.3	26 ± 6
Odontopygidae				
Chaleponcus limbatus	0.44 ± 0.04	30 ± 7	7.7 ± 1.5	14 ± 4
C. digitatus	0.88 ± 0.10	34 ± 5	7.1 ± 4.6	7 ± 9
Harpagophoridae				
Zinophora sp.	0.98 ± 0.06	32 ± 2	5.6 ± 0.8	16 ± 3

Inspection of the proportions of different foods utilized in *Acacia* savanna (Table 3) suggest that there may be a strong selection of food items which may vary according to frequency of food types and environmental conditions. In the 1990-91 rainfall season, *A. uncinatus* was most frequently observed eating seeds of the canopy tree *Acacia erubescens*. As mast-years are irregular in *A. erubescens*, this represents an opportunistic feeding tactic by *A. uncinatus* which in 1991-92 reverted to a more mixed diet. Similarly *C. carinatus* specialised on algae in 1991-92, when rainfall was 55% below the 25 year average, but also ate seeds and leaf litter in 1990-91 (Table 3). This suggests that even the more selective feeders are not obligate specialists.

During a study of the mating system in a population of *A. uncinatus* inhabiting riparian savanna in Zimbabwe (TELFORD & DANGERFIELD, 1993) several aggregations of up to 42 individuals were observed. These aggregates were not associated with the mating system but appeared to be part of the feeding tactics of immature individuals (DANGERFIELD & TELFORD,

Source : MNHN, Paris

1993). In a subsequent field experiment similar aggregates were generated by the addition of high quality food, fruits of the highveld tree *Uapaca kirkiana*, to a pine plantation habitat with limited herbaceous cover. After 48 hours, 15 to 20 millipedes, mostly *A. uncinatus*, were feeding on the fruits in an area where background densities were 0.3 individuals m^{-2}, hence the addition of high quality food attracted individuals from an area of 140 m^2 (DANGERFIELD & TELFORD, 1993).

TABLE 3. — Percentage of total feeding observations on six different food types for three species of millipede in ungrazed *Acacia* savanna in south-east Botswana in the 1990-91 and 1991-92 rainfall seasons. n is the total number of feeding observations. Data sources: DANGERFIELD, MILNER & MATTHEWS (1993); DANGERFIELD & KAUNDA (1994).

	Alloporus uncinatus		*Calostreptus carinatus*		*Chaleponcus limbatus*	
	90/91	91/92	90/91	91/92	90/91	91/92
leaf litter	12	23	30	1	16	22
seeds	41	6	20	0	30	11
grass litter	22	11	10	1	30	24
Aloe grandidentata	5	15	0	0	9	11
algae/soil	19	31	39	97	15	15
faeces	0	14	0	0	0	16
n	58	131	84	75	107	117

In savannas the distribution of high quality food resources for detritivores is spatially and temporally heterogeneous. High quality leaf litter often decays rapidly at the beginning of the rainy season (M. J. SWIFT, *pers. comm.*) whilst faeces, fruits and fungal fruiting bodies are spatially patchy and ephemeral. Such conditions would favour the evolution of opportunistic feeding tactics in detritivores that would occasionally give the impression of considerable specialisation (e.g. *C. carinatus*, Table 3). In turn, such a tactic requires cost effective mobility and sophisticated sensory discrimination mechanisms.

CONSEQUENCES OF FEEDING ACTIVITY

Combinations of millipede abundance, activity, body mass, faecal pellet production rate and pellet mass show that savanna millipedes produce 30 to 60 g m^{-2},of faecal material annually, which may be up to 40% of the litter standing crop (DANGERFIELD & MILNER, in press). Because of changes in particle size this conversion of leaf litter to faeces promotes moisture retention (MCBRAYER, 1973) and, given the importance of moisture to decomposition processes (SWIFT, HEAL & ANDERSON, 1979), faecal pellets are likely to decompose faster than uningested leaf litter. As the greater proportion of leaf litter is ingested during the first two months of the rainfall season (DANGERFIELD & TELFORD, 1991) the decomposition of litter is enhanced at a time when the nutrient demand of the vegetation is high in response to the seasonal growth of perennials and establishment of annual plants (MALAISSE, 1978). Millipedes may thus be a factor in the evolved synchrony between nutrient release and uptake typical of natural systems on poor soils where the bulk of the nutrients are stored in the vegetation and transient

Source : MNHN, Paris

soil organic matter. A reduction in millipede abundance due to land use changes (LAVELLE & PASHANASI, 1989; DANGERFIELD, 1990) would contribute to the disruption of this synchrony.

This effect on nutrient cycling combined with heterogeneous distribution of millipedes, including feeding aggregations, suggest that millipede feeding activities may reinforce small-scale patterns in the vegetation (e.g. BELSKY, 1983) and nutrient dynamics (CAMPBELL *et al.*, 1988) that already exist in savannas by enhancing plant growth in areas favoured by millipedes. Such a process would be analogous to the effect of nutrient accumulation in termitaria (see review by JONES, 1990). Experimental studies on millipede micro-distribution and correlations with the distribution of root systems and soil nutrients would provide an important test of the evolution of plant responses to the effects of soil fauna.

SPECIES DIVERSITY AND COMPETITION

Collections of surface active individuals from various savanna habitats contained between one and five millipede species (DANGERFIELD & TELFORD, 1992). Repeated observations, cryptozoan trap sampling (sensu COLE, 1946) together with hand sorting of soil samples suggest that total millipede species richness can be as high as 10 in some habitats.

Managed habitats have fewer millipede species than the natural systems from which they were derived, a pattern seen in other soil fauna groups (DANGERFIELD, 1990), and the rare species in the natural systems appear to be those that are lost. Cosmopolitan species such as *A. uncinatus* and several in the genus *Chaleponcus* appear to be less affected by habitat change, although variation in abundance or behaviour between habitats have not been investigated in detail. This combination of both sensitive and robust species, together with a significant yet manageable number of species in a given habitat, makes millipedes a potentially useful taxa for the monitoring of biodiversity.

Surface living detritivores are often considered to be largely regulated by abiotic factors and rarely compete for food resources (ANDERSON, 1977; WARBURG, LINSENMAIR & BERKOVITZ, 1984). KIME & WAUTHY (1984) have shown that percentage clay and mean annual temperature are good predictors of the numerical organisation of temperate millipede assemblages. Two features of savanna millipedes suggest that biotic interactions may also be important determinants of abundance and species composition. Firstly, the ability of several species to show dietary specialisation and opportunism, a common process leading to niche separation, and thereby avoiding competition. Secondly, the differences in relative abundance of a species between habitats and the close approximation of species abundance plots to a geometric series model (DANGERFIELD & TELFORD, 1992), which suggests that resource pre-emption and competition may structure millipede assemblages. Tests of these hypotheses require long term monitoring and experimental manipulations.

MILLIPEDES IN SAVANNA ENVIRONMENTS

In strongly seasonal environments resident organisms must evolve mechanisms to survive regular periods of stress. In savannas spirostreptid millipedes avoid up to six months without rainfall by burrowing into the soil. MANTON (1977) has established that the multi-legged configuration of juliform millipedes is able to exert considerable forward force which is well suited to burrowing. In this respect large body size is advantageous. The very large (40 g live mass) *Orthoporus* spp. of the semi-arid savannas appear not to burrow but use the vent structures of *Macrotermes* and *Odontotermes* termitaria to overwinter hence there may be an upper limit to burrowing ability and size. The importance of burrowing may mean that the distribution of the larger spirostreptids, as with temperate julids (KIME & WAUTHY, 1984) may be restricted to light textured soils.

Large body size also allows considerable mobility. This is important for opportunistic feeding tactics in heterogeneous environments or to access widely spaced shelter sites. If dry

Source : MNHN, Paris

season fire has removed the litter layer emerging millipedes must either move to new areas or utilize alternative food sources such as fresh shoots or ungulate dung, likely to be available as the grass flushes in response to the nutrients released by fire. Mobility also allows for extensive and rapid dispersal. We have observed individuals cover more than 30 m in one hour and although no data are available, movement from natal habitats may be a key feature of several species. There is some evidence that in managed environments fragments of natural habitat contain higher densities of millipedes (DANGERFIELD, 1990). Such areas may act as refuges and are favoured by mobile species.

Organisms that for the most part consume poor quality foods but have life history tactics that require large adult body size are likely to be long lived, particularly if periods of active foraging are restricted. We have kept adult specimens of *A. uncinatus* in laboratory culture for 30 months without significant mortality and suspect that most species live at least four years and possibly up to 10 years. Although there is a lengthy list of potential predators (reduviid bugs, suricates, ververids, large amphibians and hornbills) few feed exclusively on millipedes. The apparent lack of intense adult mortality combined with high female fecundity of up to 600 eggs female^{-1} (DANGERFIELD & TELFORD, unpublished data) suggest that, as with other invertebrates, density-independent juvenile mortality is likely to be high.

The spirostreptid millipedes in southern African savannas offer valuable opportunities for organism centred ecological studies. The present phase of inductive research has provided information on the ecology of a little known group which invites comparisons with the juliform species living in temperate habitats. Our analyses have also generated many hypotheses, both theoretical and organism centred, that are readily testable in this system.

ACKNOWLEDGMENTS

We are very grateful to Peter CHIBATAMOTO, Trevor COOPER, Samson KAUNDA, Bowdin KING, Charity MACKYII, Tarombera MWABVU, Busani NDLELA for field and laboratory assistance.

We thank the Department of Research and Specialist Services, Zimbabwe Ministry of Lands, Agriculture and Rural Resettlement for permission to work at the Grasslands Research Station, Marondera and the Department of National Parks and Wildlife Management for a permit to collect animals from the national parks in Zimbabwe together with the research boards of the University of Botswana and the University of Zimbabwe for financial support. We are also grateful to SAREC for logistical support provided through the TSBF programme.

REFERENCES

ANDERSON, J. M., 1977. — The organisation of soil animal communities. *Ecol. Bull. (Stockholm)*, **25** : 15-23.

BANERJEE, B., 1980. — The population characteristics of the East African red-legged diplopod *Metiche tanganyciense* Kraus (Diplopoda: Spirobolidae) *Res. Popul. Ecol.*, **21** : 306-316.

BANO, K. & KRISHNAMOORTHY, R. V., 1985. — Reproductive strategy and life history of *Jonespeltis splendidus* (Verhoeff) (Diplopoda: Polydesmida). *J. Soil Biol. Ecol.*, **5** : 48-57.

BELSKY, A. J., 1983. — Small-scale pattern in grassland communities in the Serengeti National Park, Tanzania. *Vegetatio*, **55** : 141-151.

BHAKAT, S. N., 1989. — The population ecology of *Orthomorpha coarctata* (Diplopoda: Polydesmidae). *Pedobiologia*, **33** : 49-59.

CAMPBELL, B. M., SWIFT, M. J., HATTON, J. C. & FROST P. G. H., 1988. — Small-scale vegetation pattern and nutrient cycling in miombo woodland. *In*: J. T. A. VERHOEVEN, G. W. HEIL & M. J. A. MERGER, *Vegetation structure in relation to carbon and nutrient economy*. The Hague, SPB Academic Publishing : 69-85.

COLE, L. C., 1946. — A study of the cryptozoa of an Illinois woodland. *Ecol. Monogr.*, **16** : 49-86.

CRAWFORD, C. S., 1992. — Millipedes as model detritivores. *Ber. nat.-med. Verein Innsbruck*, **suppl. 10** : 277-288.

DANGERFIELD, J. M., 1990. — Abundance, biomass and diversity of soil macrofauna in savanna woodland and associated managed habitats. *Pedobiologia*, **34** : 141-151.

DANGERFIELD, J. M., 1993 — Ingestion of mineral soil/litter mixtures and faecal pellet production in the southern African millipede *Alloporus uncinatus* (Attems). *Pedobiologia*, **37** : 159-166.

DANGERFIELD, J. M. & KAUNDA, S. K., 1994 — Millipede behaviour in a savanna woodland habitat in south-east Botswana. *African J. Ecol.*, **32** : 337-342.

Source : MNHN, Paris

DANGERFIELD, J. M. & MILNER, A. E., 1993. — Ingestion and assimilation of leaf litter in some tropical millipedes. *J. Zool.* , **229** : 683-693.

DANGERFIELD, J. M. & MILNER, A. E., (in press) — Millipede faecal pellet production in selected natural and managed habitats of southern Africa: Implications for litter dynamics. *Biotropica.*

DANGERFIELD, J. M. & TELFORD S. R., 1991. — Seasonal activity patterns of Julid millipedes in Zimbabwe. *J. Trop. Ecol.*, **7** : 281-285.

DANGERFIELD, J. M. & TELFORD, S. R., 1992. — Species diversity of Julid millipedes: Between habitat comparisons within the seasonal tropics. *Pedobiologia* , **36** : 321-329.

DANGERFIELD, J. M. & TELFORD S. R., 1993. — Aggregation in the tropical millipede *Alloporus uncinatus* (Diplopoda: Spirostreptidae). *J. Zool.*, **230**.

DANGERFIELD, J. M., MILNER, A. E. & MATTHEWS, R., 1993. — Seasonal activity patterns and behaviour of juliform millipedes in south-eastern Botswana. *J. Trop. Ecol.*, **8** : 451-464.

HAACKER, U. & FUCHS, S., 1972. — Tree-climbing in pill-millipedes. *Oecologia* , **10** : 191-192.

HUNTLEY, B. J., 1982. — Southern African Savannas. *In* : B. J. HUNTLEY & B. H. WALKER, *The ecology of tropical savannas.* Berlin, Springer-Verlag : 101-119.

JONES, J. A., 1990. — Termites, soil fertility and carbon cycling in dry tropical Africa: A hypothesis. *J. Trop. Ecol.*, **6** : 291-305.

KIME, R. D. & WAUTHY, G., 1984. — Aspects of the relationship between millipedes, soil texture and temperature in deciduous forests. *Pedobiologia* , **26** : 387-402.

LAVELLE, P. & PASHANASI, B., 1989. — Soil macrofauna and land management in Peruvian Amazonia (Yurimaguas, Loreto). *Pedobiologia* , **33** : 283-291.

LAWRENCE, R. F., 1984. — *The Centipedes and Millipedes of southern Africa. A Guide.* Cape Town, A. A. Balkema, 148 pp.

LEWIS, J. G. E., 1971. — The life history and ecology of three paradoxosomatid millipedes (Diplopoda: Polydesmida) in northern Nigeria. *J. Zool.*, **165** : 431-452.

MALAISSE, F., 1978. — The miombo ecosystem. *In*: *Tropical Forest Ecosystems. Unesco/UNEP/FAO Natural Resources Research XIV* . Paris, Unesco : 589-606.

MANTON, S. M., 1977. — *The Arthropoda. Habits, Functionnal Morphology and Evolution.* Oxford, Oxford University Press, 527 pp.

MCBRAYER, J. F., 1973. — Exploitation of deciduous leaf litter by *Apheloria montana* (Diplopoda: Eurydesmidae). *Pedobiologia* , **13** : 90-98.

POBOZSNY, M., 1986. — Uber Streuzersetzungsprozesse in Hainbuchen-Eichenwäldern unter Berücksichtigung der Diplopoden. *Opusc. Zool., Budapest.*, **22** : 77-84.

REDDY, V. M., VENKATAIAH, B., 1990. — Seasonal abundance of soil-surface arthropods in relation to some meteorological and edaphic variables of the grassland and tree-planted areas in a tropical semi-arid savanna. *Int. J. Biometeorol.*, **34** : 49-59.

RUSHTON, S. P. & HASSALL, M., 1983. — The effects of food quality on the life history parameters of the terrestrial isopod *Armadillidium vulgare* (Latreille). *Oecologia* , **57** : 257-261.

SCHOLES, R. J., 1990. — The influence of soil fertility on the ecology of southern African dry savannas. *J. Biogeogr.*, **17** : 415-419.

SWIFT, M. J., HEAL O. W. & ANDERSON, J. M., (Eds) 1979. — *Decomposition in terrestrial ecosystems.* Oxford, Blackwell Scientific Publ.

TELFORD, S. R. & DANGERFIELD J. M., 1993. — Mating tactics in the tropical millipede *Alloporus uncinatus* (Diplopoda: Spirostreptidae). *Behaviour,* **124** : 45-57.

TROLLOPE, W. S. W., 1982. — Ecological effects of fire in South African savannas. *In*: B. J. HUNTLEY & B. H. WALKER, *The ecology of tropical savannas.* Berlin, Springer-Verlag : 292-306.

VOSSEN, P., 1988. — An agrometeorological contribution to quantitative and qualitative rainy season quality monitoring in Botswana. Ph. D. Thesis, State University, Gent.

WARBURG, M. R., LINSENMAIR, K. E. & BERKOVITZ, K., 1984. — The effect of climate on the distribution and abundance of isopods. *Symp. Zool. Soc. London* , **53** : 339-363.

WOOTON, R. C. & CRAWFORD, C. S., 1975. — Food, ingestion rates and assimilation in the desert millipede *Orthoporus ornatus* (Girard) (Diplopoda). *Oecologia* , **20** : 231-236.

Source : MNHN, Paris

Source : MNHN, Paris

The Diplopod Community of a Mediterranean Oak Forest in Southern France: Ecological and Evolutionary Interest

Jean-François DAVID

CNRS, Centre d'Écologie fonctionnelle et évolutive
1919, Route de Mende. B.P. 5051, F-34033 Montpellier cedex 01, France

ABSTRACT

Seven millipede species have been found in a holm oak forest (*Quercus ilex*) sampled for two years. Seasonal changes in abundance are discussed in relation to the periods of recruitment and the changes in vertical distribution of species. Details of the life cycle of *Opisthocheiron elegans* are given. The biomass of macrosaprophagous species (on average 10.5 g live mass/m^2 for *Glomeris marginata* and *Cylindroiulus caeruleocinctus*) is the highest recorded in Europe, which points to the ecological importance of millipedes in Mediterranean forests. The millipede populations from the site studied differ intraspecifically from those found further north, as shown in *Polyzonium germanicum*. The significance of this geographical variation is discussed.

RÉSUMÉ

Le peuplement de diplopodes d'une forêt de chêne-vert dans le sud de la France.

Le peuplement de diplopodes d'une forêt de chêne vert (*Quercus ilex*) est décrit après deux années d'échantillonnage. Il comprend cinq espèces régulières et deux espèces occasionnelles. Les variations saisonnières d'abondance sont examinées en liaison avec les périodes de recrutement et les variations de la distribution verticale des populations. Quelques données sur le cycle biologique d'*Opisthocheiron elegans* sont présentées. La biomasse des espèces macrosaprophages présentes — en moyenne 10.5 g/m^2 (masse fraîche) pour *Glomeris marginata* et *Cylindroiulus caeruleocinctus* — est la plus élevée de toutes celles mesurées en Europe, ce qui souligne l'importance écologique des diplopodes dans certaines forêts méditerranéennes. Les populations de diplopodes de la station étudiée se différencient intraspécifiquement de celles trouvées plus au nord, comme le montre le cas de *Polyzonium germanicum*. La signification de cette variation géographique est discutée.

INTRODUCTION

The work of JANATI-IDRISSI (1988) on litter consumption in Mediterranean ecosystems drew attention to the millipede community of the forest of Puechabon, Hérault, on limestone hills near Montpellier. Several interesting aspects emerged: firstly, the abundance of *Glomeris* and *Cylindroiulus* populations was very high; secondly, the presence of *Polyzonium germanicum* was recorded, which was surprising for a species associated with waterlogged conditions near the centre of its west-European range (DAVID, 1990).

DAVID, J.-F., 1996. — The diplopod community of a mediterranean oak forest in Southern France: ecological and evolutionary interest. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 627-634. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

As information on millipede communities in French Mediterranean forests remained scanty (BIGOT & BODOT, 1973; SAULNIER & ATHIAS-BINCHE, 1986; JANATI-IDRISSI, 1988), further investigations were carried out at Puechabon for two years. Results have been obtained on three points: (1) the seasonal changes in abundance have been described in terms of individuals and in biomass (DAVID, 1995), which will be summarized in the present paper; (2) the extraordinary abundance of macrosaprophagous species in the Mediterranean region has been confirmed; (3) some traits distinguishing the local populations from others of the same species have been underscored, as will be shown in *P. germanicum*.

SITE AND METHODS

The study site is located in the state forest of Puechabon, 25 km northwest of Montpellier, at an altitude of 260 m. The climate, though rather humid with a cool winter, is typically Mediterranean. Rainfall is minimal in summer, with a period of severe drought almost every year; the summer dryness index of EMBERGER (1943) is < 7. A red fersiallitic soil overlies karstic limestone; its clay content is high, as is the proportion of stones. The humus form is a mull, and measurements from nearby sites have given pH ≈ 7 and C/N ≈ 16 (FLORET *et al.*, 1989; MERZOUKI *et al.*, 1989). The forest is a holm oak coppice (*Quercus ilex*) with a typical understorey of shrubs and herbs made up of several tens of species (BRAUN-BLANQUET, 1936; DUGRAND, 1963).

Sampling was carried out in an area of about 3000 m^2 surrounding a cleared plot with a CNRS meteorological station. Eight samples, each including between 10 and 12 sampling units, were taken over two years: two in spring (30 April, 1991 and 1 May, 1992), two in early summer (5 June, 1991 and 23 June, 1992), two in early autumn (7 October, 1991 and 1 October, 1992) and two in winter (3 January, 1992 and 29 January, 1993). Each sampling unit consisted of two parts: (i) litter and soil down to about 2 cm deep, collected in a 25 x 25 cm quadrat (1/16 m^2); (ii) soil between 2 and 10 cm deep, collected with a cylindrical corer 10 cm in diameter (≈1/127 m^2). The largest millipedes were sorted by hand and the others extracted by Tullgren funnels in the laboratory. Species were determined according to DEMANGE (1981).

In order to assess the fresh biomass of Chilognatha, as many individuals as possible were weighed alive after cleaning on moist filter paper, then their species, sex and stadium were determined. For dead animals, the mean live mass corresponding to their species, sex and stadium was used.

The differences in abundance were compared statistically by means of parametric (STUDENT's t-test) and non-parametric (MANN-WHITNEY U-test) methods. The differences were considered significant if both tests gave a probability $P < 0.05$.

RESULTS AND DISCUSSION

The millipede species

A total of seven specifes were found at Puechabon. Four were present in all the samples: *Glomeris marginata* (Villers), *Cylindroiulus caeruleocinctus* (Wood), *Polyzonium germanicum* Brandt and *Polyxenus lagurus*[1] Linné. Another, *Opisthocheiron elegans* Ribaut, was present in seven out of eight samples. Two other species were found occasionally on the site: one specimen of *Ommatoiulus rutilans* (C. L. Koch) was collected in the samples and several others by hand, which made it possible to determine an adult male; two specimens of *Polydesmus* sp. were collected by hand.

JANATI-IDRISSI (1988) reported the presence of *Cylindroiulus londinensis* (Leach), *Ommatoiulus sabulosus* (Linné) and *Blaniulus guttulatus* (Fabr.), in addition to *G. marginata* and *P. germanicum*. In fact, *C. caeruleocinctus* was obviously mistaken for *C. londinensis*, as often happens in the literature, and there might also have been confusion of the two *Ommatoiulus* species. As for the blaniulid, it was not found during the present study.

Population density

Overall, the average number of millipedes and its standard-error, stadium I not included, was 667 ± 56 ind./m^2, 556 ± 55 of which belonged to Chilognatha and 111 ± 16 to Penicillata. The average biomass, for Chilognatha only, was 11.0 ± 1.1 g/m^2. From samples taken between

---

[1] Southern France is inhabited by the sexual form (NGUYEN DUY - JACQUEMIN, 1973).

Source : MNHN, Paris

1984 and 1986 and sorted by hand, which yielded the largest individuals, JANATI-IDRISSI (1988) had recorded a much lower number of Chilognatha (95 ind./m2 on average) but a barely lower biomass (2.8 g *dry mass*/m2, *i.e.* between 8 and 9 g/m2).

The seasonal population densities of the five main species are given in Table 1. For each season the data from the two years are pooled, as most differences between years were not significant. There were significant seasonal changes in the population density of two species: (i) the number of *G. marginata* was lower in spring than in early summer ($P < 0.05$) and early autumn ($P < 0.01$); likewise, its biomass was lower in spring than in early autumn ($P < 0.01$ for t-test; $P < 0.05$ for U-test); (ii) the number of *P. lagurus* was lower in early autumn than in early summer ($P < 0.01$) and winter ($P < 0.05$). In all other species, the seasonal variations in numbers of individuals and in biomass were not significant.

TABLE 1. — Seasonal abundance of the main millipede species at Puechabon (after DAVID, 1995). The results are in number and biomass / m2 ± standard-error. (s.u.: sampling units).

		SPRING (21 s.u.)	EARLY SUMMER (22 s.u.)	EARLY AUTUMN (22 s.u.)	WINTER (24 s.u.)	MEAN
G. marginata	Ind./m2	100 ± 16	216 ± 44	297 ± 47	228 ± 47	212 ± 22
	g/m2	4.0 ± 0.7	7.3 ± 1.6	11.5 ± 2.1	8.0 ± 2.2	7.8 ± 0.9
C. caeruleocinctus	Ind./m2	50 ± 11	124 ± 88	54 ± 11	38 ± 12	66 ± 22
	g/m2	3.3 ± 1.0	2.2 ± 1.3	3.1 ± 0.8	2.4 ± 0.9	2.7 ± 0.5
P. germanicum	Ind./m2	352 ± 124	311 ± 118	161 ± 62	247 ± 63	267 ± 47
	g/m2	0.4 ± 0.1	0.7 ± 0.2	0.4 ± 0.2	0.4 ± 0.1	0.5 ± 0.1
O. elegans	Ind./m2	21 ± 14	16 ± 10	1 ± 1	6 ± 3	11 ± 4
	g/m2	ε	ε	ε	ε	ε
P. lagurus	Ind./m2	119 ± 37	164 ± 37	42 ± 13	121 ± 30	111 ± 16
Total Diplopoda	Ind./m2	643 ± 132	831 ± 142	556 ± 76	640 ± 86	667 ± 56
Total Chilognatha	g/m2	7.8 ± 1.2	10.3 ± 2.4	15.0 ± 2.4	10.8 ± 2.5	11.0 ± 1.1

Aspects of the seasonal dynamics

Seasonal variations in population density are not easily explained, for they depend on both actual changes in abundance (*e.g.* recruitment; mortality) and apparent changes (*e.g.* burrowing into the deep soil). Both are considered in the following discussion — keeping in mind that the seasonal changes in the vertical distribution of species were measured in the daytime, and without data regarding the height of summer. The five most abundant species all exhibit different patterns.

G. marginata generally lives near to the surface, except in winter when it tends to go deeper (Fig. 1). The vertical distribution seems the same as in Great Britain, on the opposite side of its range (BOCOCK & HEATH, 1967). Recruitment occurs during warm months, as shown by the high number of stadium II individuals (8 tergites; 8 leg pairs) in the samples from early summer and early autumn. The species seems to withstand the summer drought easily, since there is a continuous increase in abundance from spring to autumn, both in number and in biomass (Table 1). On the other hand, *G. marginata* has difficulty in coping with winter cold;

Source : MNHN, Paris

while moving down in the soil, it undergoes a fall in abundance, which becomes minimal in spring (Table 1).

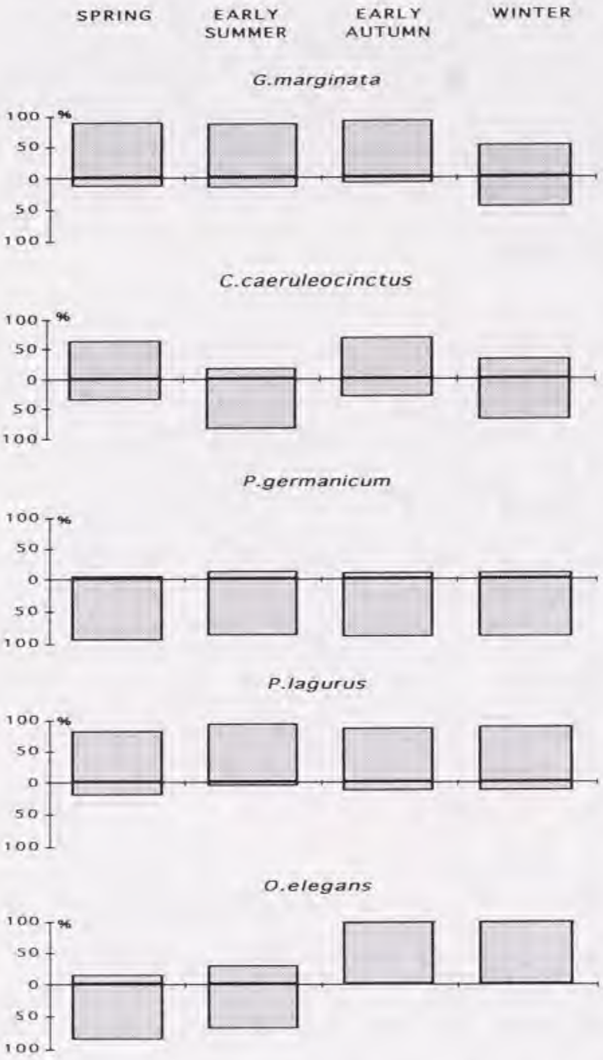


FIG. 1. — Seasonal changes in the vertical distribution of the main millipede species at Puechabon. The results are expressed as percentages of the population density (ind./m2) in two soil layers: (i) litter and top-soil down to 2 cm (above the line); (ii) soil between 2 and 10 cm deep (under the line).

C. caeruleocinctus appears to live a little deeper than *G. marginata* in spring and autumn but, like many julids in the temperate zone, it burrows markedly during summer and winter (Fig. 1). A batch of the smallest individuals (stadium IV; 3 rows of ocelli) were found in one sampling unit from the early summer of 1991, between 2 and 10 cm in depth, which may be indicative of the recruitment period. But if the young stay in the deep soil, that may explain why significant seasonal changes in density are difficult to detect.

P. germanicum is the most subterranean species at Puechabon (Fig. 1). Contrary to what could be assumed on the basis of Table 1, recruitment does not start in winter, but in summer; many brooding females were observed in spring, and stadium I individuals in early summer. But again, seasonal changes in density are difficult to detect because the whole cycle appears to occur deep in the soil; moreover, the spatial distribution is highly contagious (the variance to mean ratio reaches a maximum in this species).

In contrast, *P. lagurus* appears to remain in the litter and upper soil layer throughout the year (Fig. 1). The species seems sensitive to summer drought for its population density is significantly reduced in early autumn (Table 1). The subsequent increase during winter is suggestive of recruitment in the course of autumn, but the samples were not frequent enough to follow this fast-developing species.

The population density of *O. elegans* is low and the proportions given in Figure 1 are quite uncertain. Nevertheless, the species appears to live in the soil in spring and early summer, then to move upwards in autumn and winter (Fig. 1). These vertical displacements are concomitant with different stages in the life cycle, which looks annual at Puechabon (Table 2). Adults emerge by early autumn at the surface; they breed in winter, as shown by the appearance of the young of stadium II in January, still at the surface; then growth occurs deeper in the soil during drier months.

Ecological importance of saprophagous species

It is interesting to compare the abundance of macrosaprophagous millipedes — those which fragment litter for feeding, *i.e.*, mainly Glomerida, Julida and Polydesmida — in forests

Source : MNHN, Paris

of different climatic regions of Europe. In the Atlantic zone, the density of these species is very variable, but peak biomasses are usually below 4 g/m^2. The highest figures of fresh biomass recorded in Great Britain and northern France are, respectively, 3.9 g/m^2 in autumn samples from a mixed mull-like moder (BLOWER, 1979) and 2.3 g/m^2 in spring and autumn samples from an oak mull (DAVID, 1989). The figure of 7.5 g/m^2 in a Danish beech mull provided by BORNEBUSCH (1930) may be an overestimate, owing to the approximate value of individual biomasses. Similarly, the highest biomass figure recorded in more continental regions of western Europe is an annual mean of 4 g/m^2 for all Diplopoda, in a mixed oak wood in Austria (MEYER *et al.*, 1984).

Although data are more scarce in European regions of the Mediterranean, they are also very variable. Nevertheless, peak biomasses are higher than in the Atlantic zone, notably in climatic transition areas. IATROU (1989) has measured a density of 114 ind./m^2 for macrosaprophagous millipedes in a community of northern Greece where *Glomeris balcanica* is dominant, which should correspond to a substantial biomass (above 7.1 g/m^2, the figure for *G. balcanica* alone). The biomass of macrosaprophagous species at Puechabon is higher than all those mentioned above, on average 10.5 g/m^2 for Glomerida and Julida.

Provided that the ingestion rate is of the same order of magnitude as in the conditions prevailing in the Atlantic zone (about 10 g dry litter/g fresh mass/year — (VAN DER DRIFT, 1975; DAVID, 1987), millipedes probably play a very important role in Mediterranean forest ecosystems. So it should be very interesting to pursue the ecological studies which have been undertaken on litter consumption by millipedes in that region (BERTRAND *et al.*, 1987; JANATI-IDRISSI, 1988).

TABLE 2. — Seasonal changes in the stadial composition of *O. elegans* at Puechabon (ind./m^2). From stadium II in winter, individuals proceed to the adult stage in autumn, through stadium V in spring and stadium VII in early summer.

	STADIUM (and number of rings)							
	II (5/2)	III (7/3)	IV (10/4)	V (14/4)	VI (18/4)	VII (22/3)	VIII (25/2)	AD (27/2)
WINTER	3	1	1					1
SPRING			6	15				
EARLY SUMMER			ε		1	14	1	
EARLY AUTUMN								1

Particularity of local populations

From the taxonomic point of view, the millipede community of Puechabon does not differ from typical atlantic communities, since all the species present can be found further north. This similarity is misleading, however, for conspecific populations can be very different between the two areas. For example, if the *P. germanicum* population from the forest of Puechabon is compared with a population from the forest of Orléans, in the Centre of France, substantial differences emerge as regards colour and body size: (1) individuals from Puechabon are of paler yellowish colour than those from the forest of Orléans; (2) the difference in body size is striking, which can be shown by comparing the fresh weight of individuals in relation to their number of rings (Fig. 2); in both sexes, individuals from Puechabon are much smaller, the number of rings being equal.

Source : MNHN, Paris

Such intraspecific differences can be explained in two ways. Either there has been selection for different genotypes in the two populations, which would be closely adapted to local conditions, or there is phenotypic plasticity within the species for traits like colour and body size, in which case individuals from the two populations maintained in the same conditions would give the same phenotypes. Only cultures under controlled conditions could help to distinguish the correct explanation.

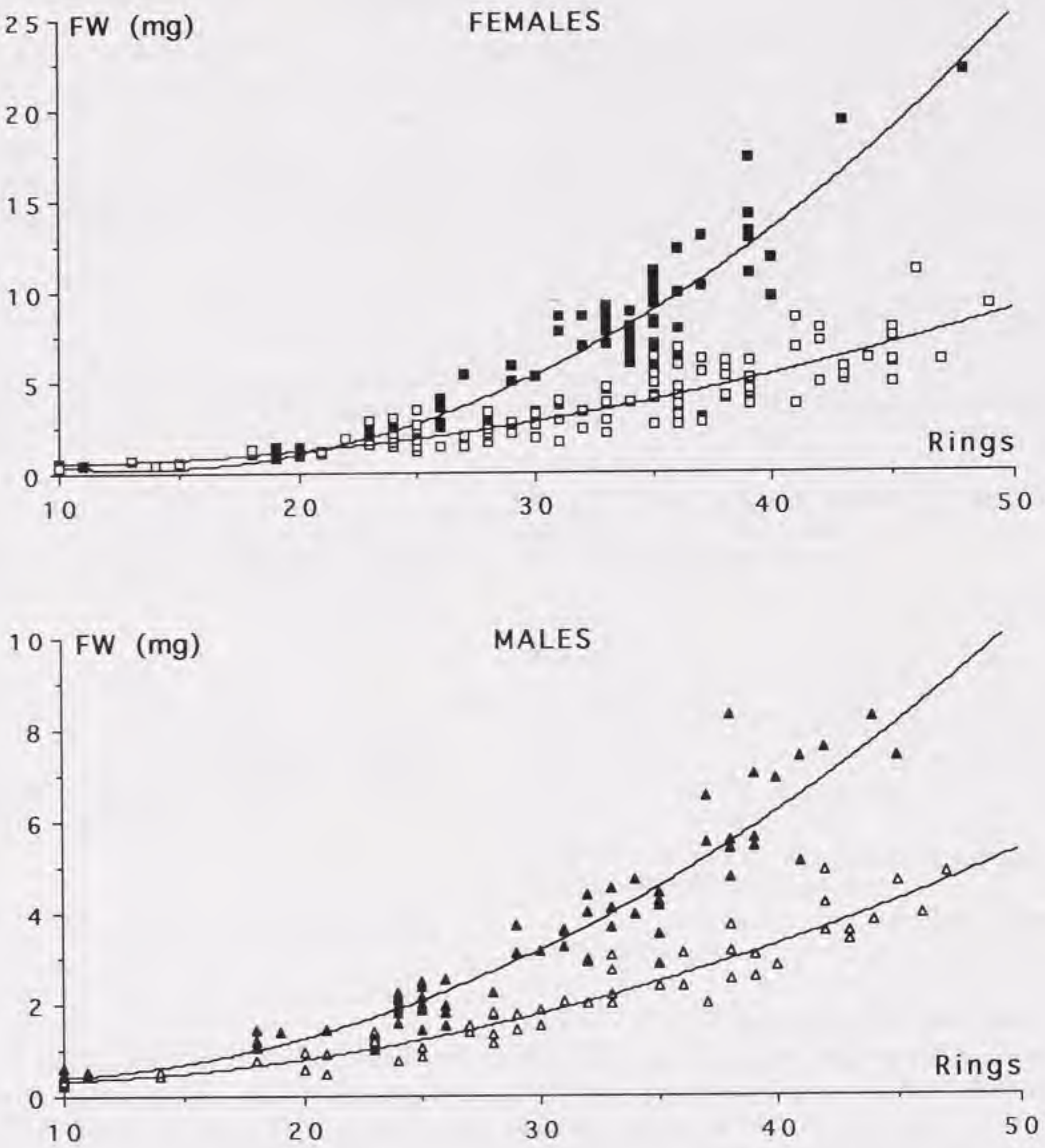


FIG. 2. — Comparison of the curvilinear regressions between fresh mass (FW) and number of podous rings, in *P. germanicum* populations from the forests of Orléans (black) and Puechabon (white). Individuals were collected from October to May on both sites.

However, the special selective forces that act at the periphery of a species range, in ecologically marginal areas, generally favour genetic differentiation of populations, regarding many morphological, physiological, behavioural or demographic traits (MAYR, 1963). As all the

Source : MNHN, Paris

species present at Puechabon but *P. lagurus* are near the driest boundary of their geographical range (MAURIÈS, 1964; MAURIES & GEOFFROY, 1982; KIME, 1990a, b), it is tempting to suggest that such a genetic differentiation has occurred. This is a very likely scenario in the case of *P. germanicum*, which is probably a small isolate at Puechabon given the species' rarity in the Montpellier region.

Irrespective of the process actually involved, different factors can exert an influence on soil animals in Mediterranean areas (DI CASTRI, 1973). On one hand, the effects of climatic factors such as summer drought can be felt in species remaining near the surface of the soil. On the other hand, constraints associated with an endogeic way of life (*e.g.* low availability of resources) may be the driving force in species which avoid the severity of climate by their burrowing behaviour. As regards *P. germanicum*, its living in the soil in the Mediterranean forest (Fig. 1) contrasts strongly with its high abundance in the litter in the forest of Orléans (DAVID & COURET, 1985). Therefore, the differences in body size and colour between the two populations — whether they are genetic adaptation or phenotypic characteristics due to acclimatory or developmental responses — may result from their living in microhabitats differing in depth rather than in climate.

ACKNOWLEDGEMENTS

I am grateful to Prof. J.-P. LUMARET (University of Montpellier III) for information on the study site; to J.-J. GEOFFROY and J.-P. MAURIÈS (MNHN, Brunoy and Paris) for the identification of some specimens; to M. GRANDJANNY and F. ROMANE (CEFE-CNRS, Montpellier) for providing local climatic data; and to H. READ for improvements in English.

REFERENCES

BERTRAND, M., JANATI-IDRISSI, A. & LUMARET, J.-P., 1987. — Etude expérimentale des facteurs de variation de la consommation de litière de *Quercus ilex* L. et *Q. pubescens* Willd. par *Glomeris marginata* (V.) (Diplopoda, Glomeridae). *Rev. Ecol. Biol. Sol*, **24** : 359-368.

BIGOT, L. & BODOT, P., 1973. — Contribution à l'étude biocœnotique de la garrigue à *Quercus coccifera*. II. Composition biotique du peuplement d'Invertébrés. *Vie & Milieu, Revue d'écologie*, **23** : 229-249.

BLOWER, J. G., 1979. — The millipede fauna of two British limestone woods. *In* : M. CAMATINI, *Myriapod Biology*, London, Academic Press : 203-214.

BOCOCK, K. L. & HEATH, J., 1967. — Feeding activity of the millipede *Glomeris marginata* (Villers) in relation to its vertical distribution in the soil. *In* : O. GRAFF & J. E. SATCHELL, *Progress in soil biology*, North Holland, Amsterdam : 233-240.

BORNEBUSCH, C. H., 1930. — The fauna of forest soil. *Forstl. Forsogsvaes. Dan.*, **11** : 1-256.

BRAUN-BLANQUET, J., 1936. — La forêt d'Yeuse languedocienne (*Quercion ilicis*). Monographie phytosociologique. *Mém. Soc. Etud. Sci. nat. Nîmes*, **5** : 1-147.

DAVID, J. F., 1987. — Consommation annuelle d'une litière de chêne par une population adulte du Diplopode *Cylindroiulus nitidus*. *Pedobiologia*, **30** : 299-310.

DAVID, J. F., 1989. — Les peuplements de Diplopodes d'une forêt tempérée : variations spatiales et stabilité dans le temps. *Rev. Ecol. Biol. Sol*, **26** : 75-90.

DAVID, J. F., 1990. — Habitat dimensions of Diplopoda in a temperate forest on acid soil. *Rev. Ecol. Biol. Sol*, **27** : 95-112.

DAVID, J. F., 1995 . — Seasonal abundance of millipedes in a Mediterranean oak forest (southern France). *Isr. J. Zool.*, **41** : 23-31.

DAVID, J. F. & COURET, T., 1985. — Le cycle biologique du Diplopode *Polyzonium germanicum* Brandt, 1831 (Polyzoniida). *Rev. Ecol. Biol. Sol*, **22** : 367-380.

DEMANGE, J. M., 1981. — *Les mille-pattes. Myriapodes*. Boubée, Paris : 284 pp.

DI CASTRI, F., 1973. — Soil animals in latitudinal and topographical gradients of Mediterranean ecosystems. *In* : F. DI CASTRI & H. A. MOONEY, *Mediterranean type ecosystems*. Berlin, Springer-Verlag : 171-190.

DUGRAND, R., 1963. — La garrigue montpelliéraine. *Bull. Soc. Languedoc. Géogr.*, **34** : 3-266.

EMBERGER, L., 1943. — Les limites de l'aire de végétation méditerranéenne en France. *Bull. Soc. Hist. nat. Toulouse*, **78** : 159-180.

FLORET, C., GALAN, M. J., LE FLOCH, E., RAPP, M. & ROMANE, F., 1989. — Organisation de la structure, de la biomasse et de la minéralomasse d'un taillis ouvert de chêne vert (*Quercus ilex* L.). *Acta Oecol., Oecol. Plant.*, **10** : 245-262.

Source : MNHN, Paris

IATROU, G. D., 1989. — Dynamics and activity of the Diplopod *Glomeris balcanica* in the soil subsystem of an evergreen sclerophyllous formation in Mt. Hortiatis. Thesis, Thessaloniki : 216 pp.

JANATI-IDRISSI, A., 1988. — Analyse du rôle des Diplopodes en région méditerranéenne et influence de l'impact humain sur leurs communautés. Thèse, Université Montpellier 3 : 229 pp.

KIME, R. D., 1990a. — Spatio-temporal distribution of European millipedes. *In* : A. MINELLI, *Proc. 7th. int. Congr. Myriapodology.* Leiden, Brill : 367-380.

KIME, R. D., 1990b. — A provisional atlas of European Myriapods Part 1. *Fauna Europaea Evertebrata I.* Luxembourg, E.I.S.: 109 pp.

MAURIÈS, J. P., 1964. — Notes sur les Diplopodes pyrénéens. I. Les *Cylindroiulus* du sous-genre *Bracheoiulus* Verhoeff. *Bull. Soc. Hist. nat. Toulouse*, **99** : 444-449.

MAURIÈS, J. P. & GEOFFROY, J. J., 1982. — Découverte dans les Causses Majeurs d'une remarquable espèce cavernicole du genre *Opisthocheiron* Ribaut, 1913 (Diplopoda, Craspedosomida, Opisthocheiridae). *Bull. Soc. Hist. nat. Toulouse*, **118** : 131-140.

MAYR, E., 1963. — *Animal species and evolution*. Cambridge, Harvard University Press, 797 pp.

MERZOUKI, A., LOSSAINT, P., RAPP, M. & BILLES, G., 1989. — L'effet d'une coupe à blanc sur la minéralisation de l'azote d'un sol rouge méditerranéen. *Rev. Ecol. Biol. Sol*, **26** : 133-154.

MEYER, E., SCHWARZENBERGER, I., STARK, G. & WECHSELBERGER, G., 1984. — Bestand und jahreszeitliche Dynamik der Bodenmakrofauna in einem inneralpinen Eichenmischwald. *Pedobiologia*, **27** : 115-132.

NGUYEN DUY - JACQUEMIN, M., 1973. — Contribution à la connaissance de l'anatomie céphalique, des formations endocrines et du développement post-embryonnaire de *Polyxenus lagurus* (Diplopodes, Pénicillates). Thèse, Université Paris 6 : 148 pp.

SAULNIER, L. & ATHIAS-BINCHE, F., 1986. — Modalités de la cicatrisation des écosystèmes méditerranéens après incendie : cas de certains Arthropodes du sol. 2. Les Myriapodes édaphiques. *Vie & Milieu, Revue d'écologie*, **36** : 191-204.

VAN DER DRIFT, J., 1975. — The significance of the millipede *Glomeris marginata* (Villers) for oak-litter decomposition and an approach of its part in energy flow. *In* : J. VANEK, *Progress in soil zoology*. The Hague, Junk : 293-298.

Source : MNHN, Paris

Centipedes (Chilopoda) of Some Forest Communities in Slovenia

Ivan KOS

Department of Biology, Biotechnical Faculty, Askerceva 2, 61000 Ljubljana, Slovenia

ABSTRACT

Centipede communities of seven forests in Slovenia were studied using the method of the quadrat sampling and extraction by modified Tullgren funnels. Three different forestal ecosystems were investigated in the southern part of Slovenia. This area is characterized by a small degree of pollution. On the three localities of *Abieti - Fagetum Dinaricum* 36 species of centipedes were found, estimated density per square meter was between 108 (± 53) and 579 (± 124). 18 species were found in *Luzulo albidae - Fagetum*, estimated density varies between 354 (± 115) and 408 (± 94). In the *Asperulo - Carpinetum* 18 species were found, estimated density was between 136 (± 34) and 218 (± 88). In the northern part of Slovenia, around the town Velenje, three different forestal ecosystem types in five localities were investigated. There is a great emission of different pollutants by steam power station in this region of Slovenia. The species diversity was lower and the density was higher than in the non-polluted localities. In the *Querco - Luzulo - Fagetum* 23 species were identified and the estimated density ranged from 230 (± 137) to 655 (± 859), in the *Bazzanio - Abietetum* 16 species were found, the density was estimated between 195 (± 122) and 640 (± 137). In the *Vaccinio myrtilli - Pinetum* 12 species were found, the density was estimated between 165 (± 66) and 345 (± 345).

RÉSUMÉ

Chilopodes de quelques communautés forestières de Slovénie.

Les peuplements de chilopodes de sept forêts de Slovénie ont été échantillonnés par la méthode des quadrats suivi d'une extraction sélective à l'aide d'appareils de type Tullgren. Trois écosystèmes forestiers ont été étudiés dans le sud de la Slovénie, caractérisée par un faible degré de pollution. Dans trois sites à *Abieti - Fagetum Dinaricum*, 36 espèces de chilopodes ont été récoltées, la densité estimée par mètre carré varie de 108 (± 53) à 579 (± 124). 18 espèces ont été trouvées dans le *Luzulo albidae - Fagetum* où la densité estimée varie de 354 (± 115) à 408 (± 94). Dans l'*Asperulo - Carpinetum* , 18 espèces ont été récoltées, dont la densité est estimée entre 136 (± 34) et 218 (± 88). Dans le nord de la Slovénie, aux environs de Velenje, trois types d'écosystèmes forestiers ont été étudiés dans cinq localités. Cette région est caractérisée par une forte émission de polluants due à l'activité d'une centrale thermique. La richesse spécifique est plus faible et la densité plus élevée que dans les sites non-pollués. Dans le *Querco - Luzulo - Fagetum*, 23 espèces ont été identifiées, la densité estimée variant de 230 (± 137) à 655 (± 859). Dans le *Bazzanio - Abietetum* , on a trouvé 16 espèces, dont la densité estimée varie de 195 (± 122) à 640 (± 137). Enfin, dans le *Vaccinio myrtilli - Pinetum*, 12 espèces ont été récoltées, leur densité estimée variant de 165 (± 66) à 345 (± 345).

INTRODUCTION

Very little is known about the communities of Centipedes (Chilopoda) from Slovenia; there are only a few records of them also from the northern part of the Balkan Peninsula. Only MATIC

KOS, I., 1996. — Centipedes (Chilopoda) of some forest communities in Slovenia. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 635-646. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

(1966) and MATIC & TEODOREANU (1966) reported data about vegetation in localities. More information is available about centipedes in certain plant communities in Europe (e.g. ALBERT, 1979, 1982; DUNGER *et al.*, 1972; FRÜND, 1983, 1987; LOKSA, 1968, 1979; MEYER *et al.*, 1984; MINELLI & IOVANE, 1987; POSER, 1988; ZAPPAROLI, 1992; WYTWER, 1992). Comparing the region of our research with other places in Europe, we must emphasize that it has some specialities because of its' geographical site. It is important that here there are numerous mixed centipede species characteristic of different biogeographical areas (KOS, 1992). Populations of these species confirm many endemic and special communities. It is very important to research them and their basic characteristics for a better knowledge of the role of a single group of animals in the environment. In Slovenia, seven forest communities were studied at 11 different localities. The species composition, species diversity, density, and dominance were determined. Only the results of the method of quadrat of soil and litter sampling are represented here.

MATERIAL AND METHODS

The sampling sites

Centipede communities were studied in two regions in Slovenia. The first lies south of Ljubljana and is characterized by a small degree of pollution and well sustained forests. In the three localities near Kocevje (Rog, 900 m a.s.l., exposure SW) and Ribnica (Kot, 700 m a.s.l., exposure E; Mala gora, 850 m a.s.l., exposure SE) the sampling was done in the *Abieti - Fagetum Dinaricum*. The soil of these sites is shallow brown with underlying deep pockets in the limestone. On the surface, many stones are present and there are also stumps and decaying tree trunks. The fourth locality is near to Kocevje (Zeljne, 700 m a.s.l., flattened). Here the forest community is *Lamio orvule - Fagetum*. On the surface, there are few stones and the soil is similar to the previous ones. The forest of *Asperulo - Carpinetum* is near Ribnica (hamlet Seljan, 700 m a.s.l., exposure SW), the soil is shallow brown and lies on the geological joint through the limestone. *Luzulo albidae - Fagetum* is near Ribnica (Zrnovec, 600 m a.s.l., exposure SW). The soil is brown, with a thick layer of humus, the geological background is from Permian - Cretaceous silicate slate. The second research region was in the north of Slovenia surrounding the town Velenje. It is known for a great emission of different pollutants by steam powered electrical plant. Here we researched three plant communities. In the first two, two localities were selected which differed in the degree of pollution. Thus, in the *Querco - Luzulo - Fagetum* the locality Veliki vrh (480 m a.s.l., exposure NE) the influence of the power station is greater than in Crnova (450 m a.s.l., exposure NW). In the *Bazzanio - Abietetum*, the less polluted locality Topolsica (450 a.s.l., exposure NW) was researched and Lajse (450 m a.s.l., exposure NW), which is more polluted. In the locality of Zavodnje *Vaccinio myrtilli - Pinetum* grows.

Sampling

From the forest soil a predetermined number of sampling units were taken (size 25x25x10 cm or 20x20x10 cm). The soil samples were taken randomly on the free surface between 8 and 12 a.m from areas, which are not covered with stones, stumps and tree trunks. Centipedes were extracted slowly on the modificated Tullgren funnels, so that the extraction lasted 18- 21 days. The specimens were extracted in ethylene glycol and later transfered to 70% ethanol for the species determination after ATTEMS (1929, 1930), EASON (1982), KOREN (1986), MATIC (1966, 1972), VERHOEFF (1937) and others. The anamorph stages of Lithobiidae could not be determined and are labelled in the tables as *L.* sp. juv. Species *Si.* n. sp. is a new species for science, species *Si.* non-*microps* is determined after VERHOEFF (1937) as *Lithonnanus microps* Mein., but is another species (EASON, KOS, in prep.). The dates of sampling and the number of sampling units are listed in the tables. The estimated density was made after ELLIOT (1977), SEBER (1982) and KREBS (1989), but the type of the distributions was not taken into account. The 95% confidence limits of the mean was calculated as $\pm$ t*SE. The density is given for a m^2 of free forest surface. The Shannon - Weaver diversity index was also calculated.

RESULTS AND DISCUSSION

Species Composition

In the study of species composition we must take samples of suitable dimensions, about 20 sampling units in size 20x20x10 cm (KOS, 1988). Otherwise the species with small densities and the species with very aggregative distribution would not be included in the samples. It is also important to consider that some centipede species prefer some habitats (FRÜND, 1983, 1987; KOS, 1988). Because of this, species which live in tree trunks, in stumps, and under stones are not detected in their real number when using soil sampling methods. These must be considered in comparing different localities and communities. The largest number of species of

Source : MNHN, Paris

centipedes was found in *Abieti - Fagetum Dinaricum*, where 23 species were present in two localities and 22 species in one. This number is much larger than is reported from other parts of Europe (ALBERT, 1982; DUNGER *et al.*, 1972; FRÜND, 1983; LOKSA, 1968, 1979; MEYER *et al.*, 1984; WYTWER, 1992). The reason for this high number could be the biogeographical situation of these communities. An open question is the influence of the limestone substrate in the Karst, with its peculiar formations, on the number of species in these communities. Also, the influence of pollutants on the number of species is yet to be studied. In the *Asperulo - Carpinetum* and *Luzulo albidae - Fagetum*, 18 species were registered. Both localities are in southern Slovenia. Around the town Velenje, most of the species were present in *Querco - Luzulo - Fagetum* (16 in one locality and 15 in another). In *Vaccinio myrtilli-Pinetum* we found 12 species, and the smallest number of species was found in *Bazzanio - Abietetum* (11 and 10 species). The results from communities mentioned are similar to those known from the middle of Europe (ALBERT, 1982; DUNGER *et al.*, 1972; FRÜND, 1983; LOKSA, 1968, 1979; MEYER *et al.*, 1984; WYTWER, 1992). The Shannon - Wieners diversity index shows the same situation; the highest is in *Abieti - Fagetum Dinaricum* (between 2.17 and 2.60). In other communities its value is lower (between 1.09 and 2.08).

Density

The density of centipedes was determined on the basis of sampling the "free" surface. The results, which present the number of animals per squere meter of "free" surface are listed in the Tables 1-10. The number is probably underestimated because of the sampling methods and extraction. When sampling, we took only the upper 10 cm of soil, but some specimens also live deeper. And at slow extraction, some specimens remain in the soil (ALBERT, 1982; FRÜND, 1987). In comparing our density results to those of others we must take into account that they probably do not show the density of animals in the surface of the forest, but in the "free" surface, which is smaller. We suppose that other authors also estimated density in this way, but this was not always emphasized in their reports.

There is no data avaliable about the density of centipedes in *Abieti - Fagetum*. The estimated number of centipedes varied between 108 (± 53) in one locality (Kot, on 8.5.1987, Table 2) and 579 (± 124) in the locality Rog (18.4.1990, Table 1). On the basis of our results we can conclude, that the density of centipedes in coniferous forest is smaller than in decidious forest. It would be interesting to study the influence of litter on the density of centipedes. Taking into account the results of some authors who also researched centipedes in different communities (ALBERT, 1982; DUNGER *et al.*, 1972; FRÜND, 1983, 1987; WYTWER, 1992), we see that in spruce forests, the density of centipedes in studied communities in Slovenia is much bigger than in other parts of Europe. Further investigations of spruce forests in this region will probably give the explanation for such big differences in density. Similar as in spruce forests, also in beech forests of studied communities, the density of centipedes was much higher than is reported by some authors from the other parts of Europe (ALBERT, 1982; FRÜND, 1983, 1987; LOKSA, 1968; WYTWER, 1990).

On the basis of the shown results (Tables 1-10), we can see some specific interconnections between different populations of centipedes in individual localities. These interconnections are related to plant communities, but the reasons for these relations are probably not only due to the plants themselves, but to the conditions in the locality as well, such as microclimate, habitat and biogeography, which the plant community also defines.

The results confirmed our previous conclusions about the great number of specific communities in the area of the northern Balkans (KOS, 1992), a characteristic of its biogeographical situation, configuration and relative well sustained environment.

The specifity is presented in species composition and in the other characteristics of communities: density, dominance, distribution of specimens, and probably reproductive potentials.

Source : MNHN, Paris

TABLE 1. — Estimated density of centipedes per square metre of free forest surface in *Abieti - Fagetum Dinaricum* in the locality Rog (near Kocevje, Slovenia) and Mala gora (near Ribnica, Slovenia). Estimated mean and 95% confidence limits are given. 8 sampling units (25x25x10 cm) were taken in Mala gora, and 6 sampling units (20x20x10 cm) in Rog. (Abbreviations, see Table 2).

	Rog						Mala gora					
	18.4.1990			6.11.1990			19.5.1987			9.9.1987		
species	avg/m2	t*se	dom	avg/m2	t*se	dom	avg/m2	t*se	dom	avg/m2	t*se	dom
B. montana	12.5	12.8	2.2	55.0	45.5	11.5	8.0	9.5	3.8	24.0	31.8	6.0
C. abbreviatus	12.5	28.5	2.2	10.0	24.8	2.1	0.0	0.0	0.0	0.0	0.0	0.0
C. linearis	0.0	0.0	0.0	0.0	0.0	0.0	12.0	19.9	5.7	3.2	4.6	0.8
C. sp.	8.3	12.0	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
C. trebevicensis	29.2	55.9	5.0	20.0	23.2	4.2	4.0	5.7	1.9	6.4	13.7	1.6
Ch. scheerpeltzi	0.0	0.0	0.0	0.0	0.0	0.0	4.0	5.7	1.9	0.0	0.0	0.0
D. carniolensis	0.0	0.0	0.0	5.0	12.4	1.0	9.9	9.2	4.8	0.0	0.0	0.0
G. insculptus	4.2	9.5	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
G. oligopus cf.	0.0	0.0	0.0	15.0	24.8	3.1	5.9	6.4	2.9	0.0	0.0	0.0
G. promontorii	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.0	9.3	2.0
G. sp.	4.2	9.5	0.7	10.0	24.8	2.1	0.0	0.0	0.0	0.0	0.0	0.0
G. flavus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	3.4	0.4
S. carniolensis	0.0	0.0	0.0	10.0	24.8	2.1	0.0	0.0	0.0	1.6	3.4	0.4
S. nemorensis	0.0	0.0	0.0	5.0	12.4	1.0	0.0	0.0	0.0	0.0	0.0	0.0
St. acuminata	16.7	12.0	2.9	15.0	24.8	3.1	1.9	4.4	1.0	4.8	5.3	1.2
St. transsilvanica	8.3	19.0	1.4	15.0	24.8	3.1	9.9	9.2	4.8	14.4	15.7	3.6
H. gottscheensis	4.2	9.5	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
L. castaneus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.2	4.6	0.8
L. dentatus	8.3	12.0	1.4	5.0	12.4	1.0	0.0	0.0	0.0	3.2	4.6	0.8
L. forficatus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
L. sp. juv.	137.5	43.6	23.7	75.0	19.6	15.6	40.2	28.2	19.0	144.0	79.7	36.0
L. lapidicola	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	3.4	0.4
L. latro	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	17.6	12.9	4.4
L. macilentus cf.	66.7	54.5	11.5	65.0	57.4	13.5	35.8	20.6	17.1	108.8	81.4	27.2
L. nodulipes	4.2	9.5	0.7	0.0	0.0	0.0	3.8	4.4	1.9	0.0	0.0	0.0
L. sp. pl2-3	0.0	0.0	0.0	5.0	12.4	1.0	1.9	4.4	1.0	1.6	3.4	0.4
Si. n.sp.	8.3	19.0	1.4	0.0	0.0	0.0	24.0	24.0	11.4	6.4	7.5	1.6
Si. non *microps*	58.3	28.2	10.1	30.0	36.1	6.3	13.9	18.2	6.7	11.2	11.4	2.8
Si. sp.	0.0	0.0	0.0	5.0	12.4	1.0	0.0	0.0	0.0	0.0	0.0	0.0
M. aeruginosus	0.0	0.0	0.0	0.0	0.0	0.0	1.9	4.4	1.0	0.0	0.0	0.0
Cry. croaticus	0.0	0.0	0.0	5.0	12.4	1.0	0.0	0.0	0.0	0.0	0.0	0.0
Cry. hortensis	108.3	50.3	18.7	85.0	84.5	17.7	20.0	14.6	9.5	22.4	18.5	0.0
Cry. parisi	58.3	38.0	10.1	45.0	45.5	9.4	12.0	17.4	5.7	16.0	12.5	0.0
Cry. rucneri cf.	29.2	27.2	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
total density	579.2	123.6	100.0	480.0	245.7	100.0	197.9	82.0	100.0	400.0	146.0	100.0
total species	17			17			15			17		
Sha-W. div.	2.325			2.444			2.450			2.170		

Source : MNHN, Paris

TABLE 2. — Estimated density of centipedes per square metre of free forest surface in *Abieti - Fagetum Dinaricum* in the locality Kot (near Ribnica). Estimated mean and 95% confidence limits are given. The sampling was done on 8.5.1987 (12 sampling units), 21.7.1987 (16 sampling units), and on 6.11.1987 (14 sampling units). The size of a sampling unit was 25x25x10 cm. Abbreviations - B: *Brachyschendyla*; C: *Clinopodes*; Ch: *Chaetechelyne* or *Chalandea*; D: *Dicellophilus*; G: *Geophilus*; S: *Schendyla*, St: *Strigamia*; E: *Eupolybothrus*, H: *Harpolithobius*; L: *Lithobius*; M: *Monotarsobius*; Si: *Sigibius*; Cry: *Cryptops*.

	8.5.1987			21.7.1987			6.11.1987		
species	avg/m2	t*se	dom	avg/m2	t*se	dom	avg/m2	t*se	dom
B. montana	4.0	4.6	3.7	5.9	8.7	2.0	17.1	9.9	7.1
C. linearis	0.0	0.0	0.00	5.0	6.7	1.7	8.0	7.9	3.3
C. trebevicensis	0.0	0.0	0.0	4.6	13.1	4.8	0.0	0.0	0.0
Ch. scheerpeltzi	0.0	0.0	0.0	5.5	6.2	2.8	0.0	0.0	0.0
D. carniolensis	9.3	9.2	8.6	4.2	3.4	1.1	4.6	3.4	1.9
G. carpophagus	0.0	0.0	0.0	3.8	2.1	0.3	0.0	0.0	0.0
G. pygmaeus	0.0	0.0	0.0	3.3	2.1	0.3	0.0	0.0	0.0
G. flavus	1.3	2.9	1.2	2.9	6.9	3.1	1.1	2.5	0.5
S. carniolensis	0.0	0.0	0.0	2.0	2.1	0.3	3.4	5.4	1.4
St. acuminata	1.3	2.9	1.2	2.5	5.3	2.0	3.4	3.9	1.4
St. transsilvanica	2.7	4.0	2.5	1.6	5.1	1.7	8.0	6.0	3.3
E. tridentinus	1.3	2.9	1.2	1.0	2.1	0.3	0.0	0.0	0.0
H. anodus	0.0	0.0	0.0	1.0	2.1	0.3	1.1	2.5	0.5
L. agilis	0.0	0.0	0.0	1.0	2.1	0.3	0.0	0.00	0.00
L. dentatus	5.3	6.6	4.9	1.9	4.3	0.7	0.0	0.0	0.0
L. sp. juv.	30.7	26.5	28.4	119.0	55.9	41.1	107.4	56.7	44.3
L. lapidicola	2.7	4.0	2.5	12.0	8.5	4.1	5.8	6.8	2.4
L. latro	2.7	4.0	2.5	5.9	6.9	2.0	5.8	5.8	2.4
L. macilentus cf.	5.3	5.0	4.9	32.0	16.8	11.0	24.0	24.2	9.9
L. nodulipes	0.0	0.0	0.0	3.0	3.4	1.1	0.0	0.00	0.00
L. sp.	1.3	2.9	1.2	0.0	0.0	0.0	0.0	0.0	0.0
M. aeruginosus	9.3	9.2	8.6	21.9	9.8	7.6	10.2	10.6	4.3
Si. n.sp.	1.3	2.9	1.2	5.0	6.7	1.7	0.0	0.0	0.0
Si. non *microps*	0.0	0.0	0.0	15.0	11.4	5.2	16.0	14.5	6.6
Cry. parisi	29.3	19.8	27.1	13.9	6.1	4.8	26.2	13.4	10.9
total density	108.0	52.7	100.0	289.9	91.7	100.0	242.2	95.6	100.0
total species	14			22			14		
Sha-W. div.	2.090			2.600			2.320		

Source : MNHN, Paris

TABLE 3. — Estimated density of centipedes per square metre of free forest surface in *Lamio-ovulae-Fagetum* in the locality Zeljne (near Kocevje). Estimated mean and 95% confidence limits are given. 6 sampling units (20x20x10 cm) were taken. (Abbreviations, see Table 2).

	18.4.1990			6.11.1990		
species	avg/m2	t*se	dom	avg/m2	t*se	dom
B. montana	33.3	28.2	10.1	62.5	52.6	11.2
C. abbreviatus	8.3	19.0	2.5	16.7	24.1	3.0
D. carniolensis	0.0	0.0	0.0	12.5	12.8	2.3
S. carniolensis	0.0	0.0	0.0	8.3	19.0	1.5
St. acuminata	0.0	0.0	0.0	8.3	12.0	1.5
St. transsilvanica	4.2	9.5	1.3	16.7	28.2	3.0
H. anodus	12.5	28.5	3.8	0.0	0.0	0.0
L. agilis	0.0	0.0	0.0	4.2	9.5	0.8
L. sp. juv.	91.7	74.6	27.9	145.8	78.5	26.2
L. macilentus cf.	75.0	76.6	22.8	62.5	43.6	11.2
L. melanops	0.0	0.0	0.0	8.3	12.0	1.5
L. pygmaeus	25.0	20.8	7.6	0.0	0.0	0.0
M. aeruginosus	50.0	48.9	15.2	179.2	124.5	32.2
M. sp.	0.0	0.0	0.0	4.2	9.5	0.8
Si. non *microps*	29.2	37.3	8.9	0.0	0.0	0.0
Cry. hortensis	4.2	9.5	1.3	0.0	0.0	0.0
Cry. parisi	12.5	19.5	3.8	37.5	35.3	6.7
total density	329.2	207.5	100.0	556.7	238.3	100.0
total species	10			12		
Sha-W. div.	1.970			1.470		

Source : MNHN, Paris

TABLE 4. — Estimated density of centipedes per square metre of free forest surface in *Asperulo - Carpinetum* in the locality Seljan (near Ribnica). Estimated mean and 95% confidence limits are given. 8 sampling units (25x25x10 cm) were taken. (Abbreviations, see Table 2).

	19.5.1987			9.9.1987		
species	avg/m2	t*se	dom	avg/m2	t*se	dom
B. montana	24.0	13.4	11.0	8.0	7.7	5.9
C. flavidus	5.9	9.2	2.8	0.0	0.0	0.0
C. linearis	4.0	5.7	1.8	1.6	3.4	1.2
C. trebevicensis	13.9	18.6	6.4	1.6	3.4	1.2
D. carniolensis	8.0	9.5	3.7	4.8	5.3	3.5
G. flavus	45.9	40.3	21.1	33.6	22.5	24.7
S. carniolensis	1.9	4.4	0.9	0.0	0.0	0.0
St. crassipes	1.9	4.4	0.9	1.6	3.4	1.2
St. transsilvanica	1.9	4.4	0.9	3.2	6.9	2.4
L. sp. juv.	41.9	25.0	19.3	32.0	26.5	23.5
L. lapidicola	1.9	4.4	0.9	0.0	0.0	0.0
L. nodulipes	0.0	0.0	0.0	1.6	3.4	1.2
L. macilentus cf.	16.0	13.3	7.3	20.8	15.3	15.3
L. tricuspis	1.9	4.4	0.9	0.0	0.0	0.0
M. aeruginosus	21.9	25.8	10.1	6.4	13.7	4.7
Si. n.sp.	4.0	5.7	1.8	3.2	4.6	2.4
Si. non *microps*	8.0	9.5	3.7	14.4	13.9	10.6
Cry. hortensis	0.0	0.0	0.0	1.6	3.4	1.2
Cry. parisi	20.0	25.6	9.2	1.6	3.4	1.2
total density	217.9	88.2	100.0	136.0	33.6	100.0
total species	16			14		
Sha-W. div.	2.085			1.737		

Source : MNHN, Paris

TABLE 5. — Estimated density of centipedes per square metre of free forest surface in *Luzulo albidae - Fagetum* in the locality Zrnovec (near Ribnica). Estimated mean and 95% confidence limits are given. 6 sampling units (25x25x10 cm) were taken. (Abbreviations, see Table 2).

	19.5.1987			11.9.1987		
	avg/m2	t*se	dom	avg/m2	t*se	dom
B. montana	88.0	53.1	24.9	53.9	29.8	13.2
C. trebevicensis	53.9	41.2	15.2	61.9	34.4	15.2
Ch. illyriaca	0.0	0.0	0.0	1.9	4.4	0.5
D. carniolensis	9.9	6.4	2.8	9.9	6.4	2.4
G. oligopus	1.9	4.4	0.5	0.0	0.0	0.0
St. acuminata	0.0	0.0	0.0	8.0	9.5	2.0
St. transsilvanica	1.9	4.4	0.5	0.0	0.0	0.0
L. castaneus	1.9	4.4	0.5	0.0	0.0	0.0
L. forficatus	1.9	4.4	0.5	1.9	4.4	0.5
L. sp. juv.	33.9	30.2	9.6	65.9	31.7	16.2
L. lapidicola	4.0	5.7	1.1	17.9	10.4	4.4
L. latro	1.9	4.4	0.5	0.0	0.0	0.0
L. macilentus cf.	64.0	34.2	18.1	88.0	55.1	21.6
L. melanops	1.9	4.4	0.5	0.0	0.0	0.0
L. pygmaeus	1.9	4.4	0.5	0.0	0.0	0.0
Si. non *microps*	24.0	23.1	6.8	12.0	8.8	2.9
M. aeruginosus	33.9	22.6	9.6	53.9	25.8	13.2
Cry. hortensis	8.0	13.4	2.3	5.9	13.2	1.4
Cry. parisi	20.0	14.6	5.6	25.9	21.1	6.3
total density	354.0	115.3	100.0	408.0	94.3	100.0
total species	16			12		
Sha-W. div.	2.055			2.030		

Source : MNHN, Paris

TABLE 6. — Estimated density of centipedes per square metre of free forest surface in *Vaccinio myrtilli- Pinetum* in the locality Zavodnje (near Velenje). Estimated mean and 95% confidence limits are given. 6 sampling units (20x20x10 cm) were taken. (Abbreviations, see Table 2).

	22.6.1990			23.10.1990			21.3.1991		
species	avg/m2	t*se	dom	avg/m2	t*se	dom	avg/m2	t*se	dom
B. montana	0.0	0.0	0.0	50.0	41.5	14.5	20.0	21.9	12.1
C. abbreviatus	5.0	11.7	1.8	0.0	0.0	0.0	0.0	0.0	0.0
C. trebevicensis	140.0	115.2	50.9	20.0	34.2	5.8	5.0	11.7	3.0
S. nemorensis	0.0	0.0	0.0	25.0	37.1	7.2	25.0	37.1	15.2
S. carniolensis	0.0	0.0	0.0	25.0	45.4	7.2	15.0	23.5	9.1
St. acuminata	5.0	11.7	1.8	0.0	0.0	0.0	0.0	0.0	0.0
L. macilentus	35.0	35.2	12.7	85.0	133.2	24.6	65.0	54.4	39.4
L. latro	0.0	0.0	0.0	20.0	11.7	5.8	5.0	11.7	3.0
L. tenebrosus	15.0	23.5	5.5	15.0	35.2	4.3	0.0	0.0	0.0
L. sp. juv.	20.0	21.9	7.3	75.0	132.5	21.7	10.0	23.5	6.1
M. aeruginosus	25.0	18.5	9.1	20.0	34.2	5.8	10.0	23.5	6.1
Cry. hortensis	30.0	34.2	10.9	10.0	14.4	2.9	10.0	14.4	6.1
Cry. parisi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
total density	275.0	143.64	100.0	345.0	344.7	100.0	165.0	65.8	100.0
total species	7			9			8		
Sha-W. div.	1.402			1.978			1.613		

TABLE 7. — Estimated density of centipedes per square metre of free forest surface in *Bazzanio - Abietetum* in the locality Topolsica (near Velenje). Estimated mean and 95% confidence limits are given. 6 sampling units (20x20x10 cm) were taken. (Abbreviations, see Table 2).

	22.6.1990			23.10.1990			21.3.1991		
species	avg/m2	t*se	dom	avg/m2	t*se	dom	avg/m2	t*se	dom
B. montana	0.0	0.0	0.0	5.0	11.7	1.6	15.0	23.5	7.7
G. insculptus	43.8	78.6	11.3	75.0	41.5	23.4	10.0	14.4	5.1
G. oligopus cf.	12.5	25.4	3.2	0.0	0.0	0.0	0.0	0.0	0.0
S. nemorensis	0.0	0.0	0.0	25.0	45.4	7.8	5.0	11.7	2.6
S. carniolensis	0.0	0.0	0.0	5.0	11.7	1.6	25.0	18.5	12.8
L. forficatus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
L. sp. juv.	18.8	38.1	4.8	30.0	43.1	9.4	5.0	11.7	2.6
L. macilentus	18.8	24.3	4.8	25.0	32.1	7.8	20.0	46.9	10.3
M. aeruginosus	50.0	68.8	12.9	15.0	35.2	4.7	30.0	43.1	15.4
Cry. hortensis	137.5	44.0	35.5	140.0	73.2	43.8	85.0	75.5	43.6
Cry. parisi	6.2	12.7	1.6	0.0	0.0	0.0	0.0	0.0	0.0
total density	387.5	86.7	100.0	320.0	179.2	100.0	195.0	122.2	100.0
total species	6			7			7		
Sha-W. div.	1.367			1.417			1.506		

Source : MNHN, Paris

TABLE 8. — Estimated density of centipedes per square metre of free forest surface in *Bazzanio - Abietetum* in the locality Lajse (near Velenje). Estimated mean and 95% confidence limits are given. 6 sampling units (20x20x10 cm) were taken. (Abbreviations, see Table 2).

	22.6.1990			23.10.1990			17.6.1991		
species	avg/m2	t*se	dom	avg/m2	t*se	dom	avg/m2	t*se	dom
C. flavidus	5.0	11.7	1.1	0.0	0.0	0.0	0.0	0.0	0.0
C. trebevicensis	75.0	61.5	15.8	50.0	26.2	7.8	95.0	78.4	17.6
D. carniolensis	0.0	0.0	0.0	5.0	11.7	0.8	0.0	0.0	0.0
S. carniolensis	0.0	0.0	0.0	75.0	37.1	11.7	0.0	0.0	0.0
S. nemorensis	0.0	0.0	0.0	60.0	68.4	9.4	0.0	0.0	0.0
St. acuminata	5.0	11.7	1.1	0.0	0.0	0.0	0.0	0.0	0.0
L. dentatus	5.0	11.7	1.1	0.0	0.0	0.0	0.0	0.0	0.0
L. sp. juv.	90.0	93.8	18.9	130.0	77.4	20.3	60.0	57.5	11.1
L. macilentus	70.0	65.3	14.7	105.0	98.8	16.4	65.0	104.9	12.0
M. aeruginosus	130.0	70.4	27.4	80.0	65.3	12.5	200.0	193.0	37.0
Cry. hortensis	85.0	77.8	17.9	120.0	56.9	18.8	110.0	92.9	20.4
Cry. parisi	10.0	14.4	2.1	15.0	14.4	2.3	10.0	30.8	1.8
total density	475.0	252.2	100.0	640.0	137.0	100.0	540.0	160.6	100.0
total species	8			8			5		
Sha-W. div.	1.223			1.226			1.867		

TABLE 9. — Estimated density of centipedes per square metre of free forest surface in *Querco - Luzulo - Fagetum* in the locality Veliki vrh (near Velenje). Estimated mean and 95% confidence limits are given. 6 sampling units (20x20x10 cm) were taken. (Abbreviations, see TABLE .2).

	22.6.1990			23.10.1990			21.3.1991			17.6.1991		
species	avg/m2	t*se	dom	avg/m2	t*se	dom	avg/m2	t*se	dom	avg/m2	t*se	dom
B. montana	0.0	0.0	0.0	10.0	14.4	2.9	10.0	14.4	3.9	0.0	0.0	0.0
C. abbreviatus	0.0	0.0	0.0	25.0	58.6	7.1	10.0	14.4	3.9	0.0	0.0	0.0
C. flavidus	5.0	11.7	2.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
C. linearis	0.0	0.0	0.0	5.0	11.7	1.4	5.0	11.7	2.0	5.0	11.7	1.0
C. trebevicensis	10.0	14.4	4.3	10.0	14.4	2.9	5.0	11.7	2.0	35.0	35.2	7.1
D. carniolensis	5.0	11.7	2.2	5.0	11.7	1.4	0.0	0.0	0.0	0.0	0.0	0.0
G. oligopus cf.	10.0	23.5	4.3	5.0	11.7	1.4	20.0	21.9	7.8	15.0	23.5	3.0
St. transsilvanica	0.0	0.0	0.0	5.0	11.7	1.4	0.0	0.0	0.0	0.0	0.0	0.0
E. tridentinus	0.0	0.0	0.0	5.0	11.7	1.4	0.0	0.0	0.0	0.0	0.0	0.0
L. dentatus	0.0	0.0	0.0	5.0	11.7	1.4	10.0	23.5	3.9	0.0	0.0	0.0
L. forficatus	0.0	0.0	0.0	5.0	11.7	1.4	0.0	0.0	0.0	0.0	0.0	0.0
L. sp. juv.	25.0	45.4	10.9	85.0	104.2	24.3	85.0	122.4	33.3	220.0	261.2	44.4
L. lapidicola	0.0	0.0	0.0	5.0	11.7	1.4	0.0	0.0	0.0	0.0	0.0	0.0
L. lusitanus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.0	11.7	1.0
L. macilentus	165.0	113.7	71.7	160.0	118.2	45.7	100.0	92.7	39.2	195.0	113.4	39.4
M. aeruginosus	5.0	11.7	2.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cry. parisi	5.0	11.7	2.2	20.0	21.9	5.7	10.0	14.4	3.9	20.0	21.9	4.0
total density	230.0	136.8	100.0	350.0	194.5	100.0	255.0	241.4	100.0	495.0	344.1	100.0
total species	7			13			8			6		
Sha-W. div.	0.831			1.569			1.348			1.000		

Source : MNHN, Paris

TABLE 10. — Estimated density of centipedes per square metre of free forest surface in *Querco - Luzulo - Fagetum* in the locality Crnova (near Velenje). Estimated mean and 95% confidence limits are given. 6 sampling units (20x20x10 cm) were taken. (Abbreviations, see Table 2).

	22.6.1990			21.3.1990			21.3.1991			17.6.1991		
species	avg/m2	t*se	dom	avg/m2	t*se	dom	avg/m2	t*se	dom	avg/m2	t*se	dom
B. montana	0.0	0.0	0.0	40.0	52.4	14.0	25.0	32.8	3.8	0.0	0.0	0.0
C. abbreviatus	0.0	0.0	0.0	5.0	6.6	1.8	5.0	6.6	0.8	0.0	0.0	0.0
C. trebevicensis	15.0	19.7	4.3	10.0	13.1	3.5	0.0	0.0	0.0	0.0	0.0	0.0
D. carniolensis	0.0	0.0	0.0	5.0	6.6	1.8	5.0	6.6	0.8	5.0	6.6	1.1
G. insculptus	75.0	98.3	21.7	30.0	39.3	10.5	30.0	39.3	4.6	205.0	268.8	43.6
G. flavus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.0	6.6	1.1
S. nemorensis	0.0	0.0	0.0	0.0	0.0	0.0	10.0	13.1	1.5	0.0	0.0	0.0
St. acuminata	5.0	6.6	1.4	0.0	0.0	0.0	10.0	13.1	1.5	5.0	6.6	1.1
L. dentatus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
L. forficatus	5.0	6.6	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
L. lusitanus	5.0	6.6	1.4	0.0	0.0	0.0	10.0	13.1	1.5	20.0	26.2	4.3
L. macilentus	100.0	131.1	29.0	55.0	72.1	19.3	150.0	196.7	22.9	110.0	144.2	23.4
L. nodulipes	0.0	0.0	0.0	0.0	0.0	0.0	25.0	32.8	3.8	0.0	0.0	0.0
L. validus	10.0	13.1	2.9	5.0	6.6	1.8	0.0	0.0	0.0	10.0	13.1	2.1
L. sp. juv.	70.0	91.8	20.3	45.0	59.0	15.8	265.0	347.5	40.5	65.0	85.2	13.8
L. sp.	5.0	6.6	1.4	0.0	0.0	0.0	10.0	13.1	1.5	0.0	0.0	0.0
H. sp.	0.0	0.0	0.0	0.0	0.0	0.0	5.0	6.6	0.8	0.0	0.0	0.0
Cry. hortensis	55.0	72.1	15.9	90.0	118.0	31.6	105.0	137.7	16.0	45.0	59.0	9.6
total density	345.0	452.4	100.0	285.0	373.7	100.0	655.0	858.9	100.0	470.0	616.3	100.0
total species	9			8			12			8		
Sha-W. div.	1.615			1.638			1.864			1.345		

REFERENCES

ALBERT, A. M., 1979. — Chilopoda as part of the predatory macroarthropod Fauna in forests: Abundance, Life-cycle, Biomass, and Metabolism. *In*: M. CAMATINI, *Myriapod Biology*. London, Academic Press : 215-231.

ALBERT, A. M., 1982. — Species spectrum and dispersion patterns of Chilopods in Solling habitats. *Pedobiologia*, **23** : 337-347.

ATTEMS, C., 1929. — Myriapoda. I. Geophilomorpha. *Das Tierreich*, **52** : 1-388.

ATTEMS, C., 1930. — Myriapoda II. Scolopendromorpha. *Das Tierreich*, **54** : 1-308.

DUNGER, W., ENGELMANN, I. & SCHNEIDER R., 1972. — Untersuchungen zur Langzeitwirkung von Industrie - Emissionen auf Böden, Vegetation und Bodenfauna des Neitzetales bei Ostitz/Oberlausitz. *Abh. Ber. Natur. Görlitz* , **47** : 1-40.

EASON, E. H., 1982. — A review of the North-West Lithobiomorpha with a revised key to their identification. *Zool. J. Linn. Soc.*, **74** : 9-33.

ELLIOT, J. M., 1977. — Some methods for the Statistical Analysis of samples of Benthic Invertebrates. *Freshwater Biological Association Sci. Publication* , **25** : 1-157.

FRÜND, H. C., 1983. — Untersuchungen zur Koexistenz verschiedener Chilopodenarten im Waldboden. Dissertation, Würtzburg, 164 pp.

FRÜND, H. C., 1987. — Räumliche Verteilung und Koexistenz der Chilopoden in einem Buchen-Altbestand. *Pedobiologia*, **30** : 19-29.

KOREN, A., 1986. — Die Chilopoden-Fauna von Kärnten und Osttirol, Teil 1, Geophilomorpha, Scolopendromorpha.- Verlag des Naturwiss. Vereins für Kärnten, Klagenfurt, 87 pp.

KOS, I., 1988. — The problems of quality and quantity sampling of centipedes (Chilopoda). Ljubljana, University of Ljubljana, Biotech. Faculty, Department of Biology, 85 pp. (in Slovene).

Source : MNHN, Paris

KOS, I., 1992. — A Review of Taxonomy, Geographical Distribution and Ecology of the Centipedes of Yugoslavia (Myriapoda, Chilopoda). [*In*: E. Meyer, K. Thaler, W. Schedl , Advances in Myriapodology.] *Ber. nat.-med. Verein Innsbruck*, **suppl. 10** : 353-360.

KREBS, J. R., 1989. — *Ecological methodology*. New-York, Harper Collins Publishers, 654 pp.

LOKSA, I., 1968. — Quantitative Makrofauna-Untersuchungen in den Waldboden des Bukkgebirges (Ungarn). *Ann. Univ. Sci. Budapest*, **9-10** : 265-289.

LOKSA, I., 1979. — Quantitative Untersuchungen über die Makrofauna der Laubstreu in Zerreichen- und Hainsimen-Eichen Beständen des Bükkergebirges. *Opusc. Zool. Budapest*, **16**: 87-96.

MATIC, Z., 1966. — Clasa Chilopoda, Subclasa Anamorpha. *Fauna Republicii socialiste Romania*, **6** : 1-272.

MATIC, Z., 1972. — Clasa Chilopoda , Subclasa Epimorpha. *Fauna Republicii socialiste Romania*, **6** : 1-224.

MATIC, Z. & TEODOREANU, M., 1966. — Contribution à la connaissance des Lithobiides (Chilopoda-Lithobiidae) de Croatie. *Biol. Glasnik*, **19** : 19-26.

MEYER, E., SCHWARZENBERGER, I., STARK, G. & WECHSELBERGER, G., 1984. — Bestand und jahreszeitliche Dynamik der Bodenmakrofauna in einem inneralpinen Eichenmischwald (Tirol, Österreich). *Pedobiologia*, **27 :** 115-132.

MINELLI, A. & IOVANE, E., 1987. — Preferences and taxocenoses of Italian centipedes (Chilopoda). *Boll. Mus. civ. St. nat. Venezia* , **37** : 7-34.

POSER, T., 1988. — Chilopoden als Prädatoren in einem Laubwald. *Pedobiologia*, **31** : 261-281.

SEBER, G. A. F., 1982. — *The Estimation of Animal Abundance and related Parameters*. London, Charles Griffin & Company Ltd., 654 pp.

VERHOEFF, K. W., 1937. — Chilopoden-Studien. Zur Kenntnis der Lithobiiden. *Archiv für Naturgeschichte*, **6** : 171-257.

WYTWER, J., 1990. — Centipedes (Chilopoda) of linden - oak - hornbeam forests (*Tilio - Carpinetum*) and the thermophilous oak forests (*Potentillo albae - Quercetum*) of Mazovian Lowland. *Fragm. Faun.*, **32** :73-94.

WYTWER, J., 1992. — Chilopoda Communities of the Fresh Pine Forests of Poland. [*In* : E. MEYER, K. THALER, W. SCHEDL, *Advances in Myriapodology*.] *Ber. nat.-med. Verein Innsbruck*, **suppl. 10** : 205-211.

ZAPPAROLI, M., 1992. — Preliminary Data on Centipede Communities of *Quercetea ilicis* and *Fagetalia sylvaticae* in Central Italy. [*In*: E. MEYER, K. THALER, W. Schedl, *Advances in Myriapodology*] *Ber. nat.-med. Verein Innsbruck*, **suppl. 10** : 197-204.

Source : MNHN, Paris

Changes in the Millipede (Diplopoda) Community during Secondary Succession from a Wheat Field to a Beechwood on Limestone

Stefan SCHEU

II. Zoologisches Institut, Abteilung Ökologie, Berliner Str. 28, 37073 Göttingen, Germany

ABSTRACT

The diplopod communities of five sites, which were chosen to represent different stages of secondary succession from a wheat field to a beechwood on limestone (wheat field, 4 year old fallow, 11 year old fallow, ca 50 year old fallow, beechwood), were studied for 2 years. The sites were located in close proximity on a limestone plateau east of Göttingen (southern Lower Saxonia, Germany). Diplopods were extracted by heat from soil cores four times a year. A total of 12 species were found: *Allajulus nitidus*, *Cylindroiulus caeruleocinctus*, *Leptoiulus belgicus*, *Unciger foetidus*, *Tachypodoiulus niger*, *Ommatoiulus sabulosus*, *Blaniulus guttulatus*, *Mycogona germanicum*, *Glomeris marginata*, *Glomeris conspersa*, *Stygioglomeris crinita*, *Polydesmus inconstans*. Number of species, density and biomass increased up to the 11 year old fallow stage. They were considerably lower in the 50 year old fallow (ash dominated wood) and seemed to have increased again until the formation of the climax ecosystem of the beechwood. In contrast to succession theory, no continuous change in species composition occurred; rather, diplopods flourished at intermediate stages of secondary succession. Changes in community structure are discussed and related to environmental factors. Canonical correspondence analysis indicated the great importance of the amount of litter and of humidity for the species composition of diplopods. The most important determining factor for low diversity, density and biomass of millipedes at the 50 year old fallow is assumed to be the absence of a litter layer during summer.

RÉSUMÉ

Variations dans un peuplement de diplopodes au cours d'une succession secondaire, d'un champ de blé à une hêtraie sur calcaire.

Les peuplements de diplopodes ont été étudiés pendant deux ans dans cinq sites voisins, représentatifs des différents stades d'une succession allant d'un champ de blé à une hêtraie sur calcaire (champ de blé, jachère de 4 ans, jachère de 11 ans, friche de 50 ans, forêt de hêtres). Les stations sont situées sur un plateau calcaire à l'est de Göttingen (Allemagne). Les diplopodes ont été obtenus par échantillonage de carottes de sol et extraction sélective 4 fois par an. Douze espèces ont été récoltées : *Allajulus nitidus*, *Cylindroiulus caeruleocinctus*, *Leptoiulus belgicus*, *Unciger foetidus*, *Tachypodoiulus niger*, *Ommatoiulus sabulosus*, *Blaniulus guttulatus*, *Mycogona germanicum*, *Glomeris marginata*, *Glomeris conspersa*, *Stygioglomeris crinita*, *Polydesmus inconstans*. La richesse spécifique, la densité et la biomasse augmentent jusqu'au stade jachère de 11 ans. Elles sont nettement plus faibles dans la friche de 50 ans (Frêne dominant) et semblent de nouveau augmenter jusqu'à la formation forestière "climacique" de la hêtraie. A l'encontre de la théorie des successions, aucun changement continu n'apparaît dans la composition spécifique ; on observe plutôt un développement florissant du peuplement de diplopodes durant les stades intermédiaires de la succession. Les variations de cette structure sont discutées et mises en relation avec les facteurs environnementaux. Une analyse de correspondances canonique montre la grande importance de l'apport de litière et de l'humidité dans la composition spécifique des diplopodes. Le

SCHEU, S., 1996. — Changes in the millipede (Diplopoda) community during secondary succession from a wheat field to a beechwood on limestone. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 647-656. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

facteur déterminant les faibles diversité, densité et biomasse de diplopodes dans la friche de 50 ans semble être l'absence de litière durant l'été.

INTRODUCTION

Diplopod communities of forest ecosystems (DUNGER, 1958; BLOWER, 1979; GEOFFROY, 1981; MEYER *et al.*, 1984; AXELSSON *et al.*, 1984) and arable fields (HERBKE, 1962; PETERS, 1984; KLINGER, 1992) have been frequently investigated. In addition, diplopods on restored mining soils found considerable attention (DUNGER, 1968; NEUMANN, 1971; DUNGER, & VOIGTLÄNDER, 1990). In contrast, little is known about changes in diplopod communities during secondary succession, e.g. after cessation of cultivation (TAJOVSKY, 1990).

Studies on secondary succession up to the climax are, for practical reasons, usually performed at different sites representing different stages of secondary succession. In the present study five sites were chosen to investigate changes in species composition, density and biomass of diplopods during secondary succession from an arable field to the climax ecosystem of a beechwood (*Fagus sylvatica* L.). The sites were located on a limestone plateau east of Göttingen (southern Lower Saxonia, Germany), most of them in close vicinity. The first site was an arable field which had been planted with wheat. The second and third sites had been left uncultivated for 4 and 11 years, respectively. The fourth site had been left abandened for ca 50 years and a tree layer mainly of ash (*Fraxinus excelsior* L.) had grown up at this site. The fifth site was a beechwood which has been studied intensively (cf. SCHAEFER, 1991).

The present study forms part of a project which investigated changes in density and biomass of soil animals during secondary succession in combination with functional aspects of soil invertebrates for carbon turnover and nutrient cycling (SCHEU 1990a, b, 1992; SCHULZ, 1992; WOLTERS, in prep.). The aim of the present study was to get a closer understanding of the factors responsible for changes in the millipede community during secondary succession.

MATERIALS AND METHODS

The sites

Five sites representing different successional stages from a wheat field to a beechwood were investigated. The sites were located on a limestone plateau (360-420 m) east of Göttingen (Lower Saxonia, Germany). The wheat field was planted with wheat during the investigations. In general, a rotation of wheat, barley and rape has been planted on that field during the previous 20 years. Straw residues were burnt in autumn and the field worked with a disk cultivator. The second site (first fallow) had been left uncultivated for 4 years until 1987. The flora consisted of a mixture of weeds and grasses. The third site (second fallow) had been left uncultivated for 11 years and grasses dominated at this site. The floral composition indicated a decrease in nitrogen supply until this stage (cf. SCHEU 1990b). The fourth site (third fallow) had been left uncultivated for ca 50 years and was now an ash (*F. excelsior*) dominated wood. Ash trees had overgrown shrubs which were still present but in a stage of die back. The fifth site was a ca 130 year old beechwood (*F. sylvatica*) which has been described in more detail in SCHAEFER (1991). More details on the other sites can be found in SCHEU (1990a, 1992).

The climate in the study area is characterized by mild winters and humid summers. The annual mean temperature in Göttingen is 8.7°C and the annual mean precipitation 613 mm. Variation among years is considerable and there might be longer frost periods in winter and dry periods in summer; the former was the case in February 1987, whereas the latter occurred in May and to a lesser extent also in August 1988 (Fig. 1).

The soil water content varied during the year with a maximum in late winter and spring (Fig. 2). Variation was most pronounced in the litter layer and similar in the 0-3 and 3-6 cm soil depths. Generally, the water content of the soil was similar in the arable field and the fallow sites and considerably lower than in the beechwood.

The amount of carbon and nitrogen (determined by an elemental analyser; Carlo Erba, Milano, Italy) in 0-3 and in 3-6 cm soil depth was similar in the arable field and the two younger fallow sites and considerably lower than in the ash dominated wood and the beechwood (Fig. 3). The increase in the amounts of carbon and nitrogen in the two woodlands was caused by an accumulation of humus in the upper soil layers of these ecosystems which was accompanied by a decrease in soil bulk density. Mean annual amount of carbon and nitrogen in the litter layer was at a maximum in the fallow sites but varied considerably during the year. Litter material at the first fallow consisted mainly of weed residues, whereas grass leaf litter dominated at the second fallow. Litter materials estimated are presumably somewhat too high, particularly for the 4 year old fallow, because the above ground vegetation was partly included in material taken as litter.

Source : MNHN, Paris

In the ash wood most of the litter consisted of small twigs and branches from overgrown shrubs, the leaf litter had disappeared almost entirely by spring. In the beechwood a litter layer of beech leaves was present throughout the year.

Faunal investigations

Soil cores of 0.036 m^2 were taken from the study sites and separated into litter layer, 0-3 and 3-6 cm soil depth in the field. Eight randomly distributed samples were taken at 3 month intervals from October, 1986 to October, 1988 except for the third fallow which was investigated from October, 1987 to October, 1988 only. Diplopods were extracted by heat using a modified Kempson extractor (KEMPSON *et al.*, 1963, SCHAUERMANN, 1982) and determined to species level. The biomass was estimated using regressions between the body diameter and ash free dry mass established by SPRENGEL (1986) for *Mycogona germanicum* (Verhoeff, 1897) and *Allajulus nitidus* (Verhoeff, 1891). Biomass of *Cylindroiulus caeruleocinctus* (Wood, 1864), *Leptoiulus belgicus* (Latzel, 1844), *Unciger foetidus* (C. L. Koch, 1838), *Tachypodoiulus niger* (Leach, 1815), *Ommatoiulus sabulosus* (Linné, 1758), *Blaniulus guttulatus* (Fabricius, 1798) and *Polydesmus inconstans* Latzel, 1884 was estimated using the formula for *A. nitidus*. For *Glomeris marginata* (Villers, 1789) and *G. conspersa* (C. L. Koch, 1847) regressions between the width of the collum and ash free dry mass were used (SPRENGEL, 1986). The regression for *G. marginata* was also used to calculate the biomass of *Stygioglomeris crinita* Bröleman, 1913.

Statistical analysis

Canonical correspondence analysis (CCA, TER BRAAK, 1988) was used to ordinate samples and to relate diplopod data to environmental factors. Environmental factors (water content, carbon content, nitrogen content, C/N ratio, amount of carbon, amount of nitrogen) were determined from the litter material, 0-3 and 3-6 cm soil depth of small soil cores taken in close vicinity to the core for faunal extractions. Only four cores were taken at each sampling date at each site for determination of environmental factors and therefore, only diplopods from the adjacent four cores were ordinated. The water content in 3-6 cm soil depth was excluded from the analysis because of the collinearity with the water content in 0-3 cm (cf. Fig. 2). The amount and content of carbon and nitrogen in 0-3 and 3-6 cm soil depth was excluded because the correlation with species axes was poor ($r < 0.3$). Eigenvalues obtained by CCA ordination were compared with those of DCA (detrended correspondence analysis; cf. TER BRAAK, 1988) ordination to estimate the relevance of the environmental factors included in the analysis.

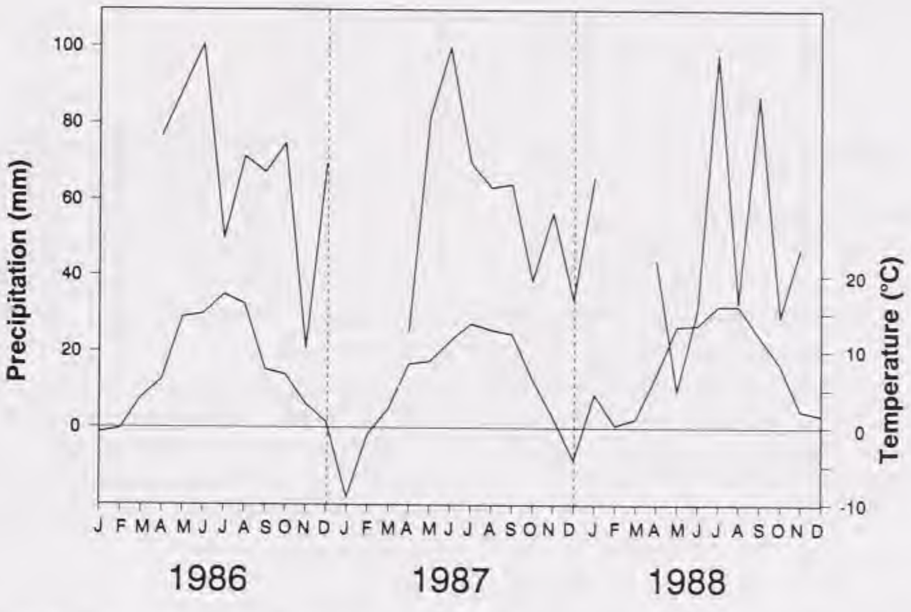


FIG. 1. — Monthly mean temperature and precipitation at the study sites in 1986-1988 (data were kindly provided by the Institute for Soil Science, Göttingen).

RESULTS

Species composition

A total of 12 diplopod species were found. Six species of Julidae (*A. nitidus*, *C. caeruleocinctus*, *L. belgicus*, *U. foetidus*, *T. niger*, *O. sabulosus*) and three Glomeridae (*G. marginata*, *G. conspersa*, *S. crinita*). The other three species belonged to three different

Source : MNHN, Paris

families: *B. guttulatus* (Blaniulidae), *M. germanicum* (Chordeumatidae), *P. inconstans* (Polydesmidae).

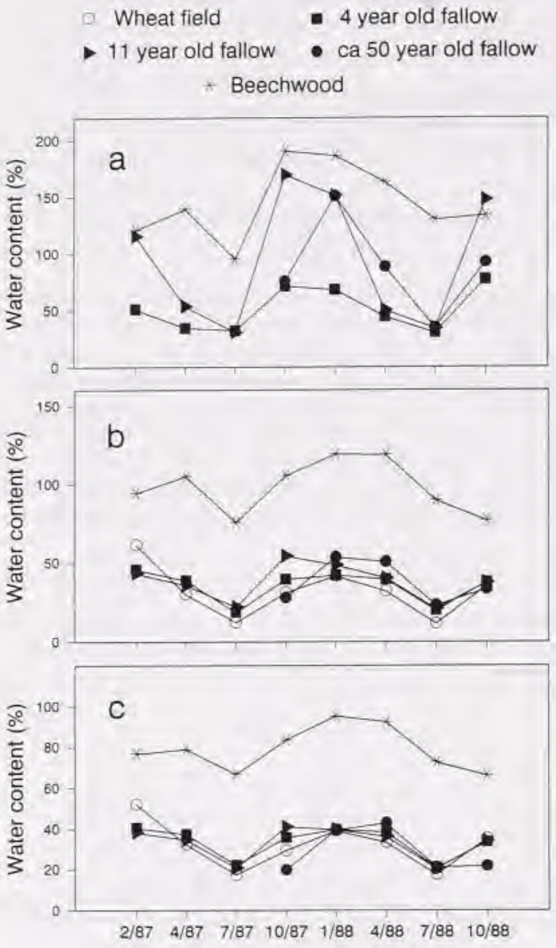


FIG. 2. — Changes in gravimetric soil water content in the litter layer (a), 0-3 (b) and 3-6 cm soil depth (c) at five sites representing different stages of secondary succession during 1987 and 1988.

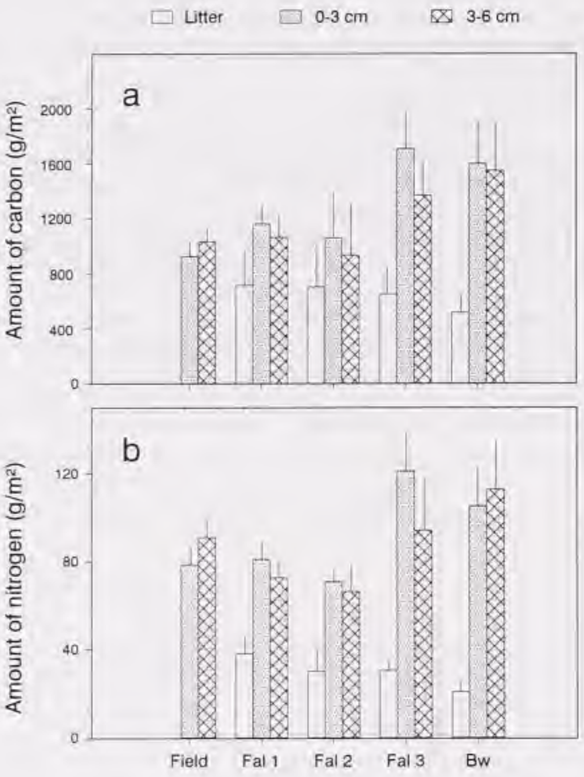


FIG. 3. — Amount of carbon (a) and nitrogen (b) in the litter layer, 0-3 and 3-6 cm soil depth of the study sites (means + SD of samples taken at 3 month intervals during 1987 and 1988; Field, wheat field; Fal 1, 4 year old fallow; Fal 2, 11 year old fallow; Fal 3, ca 50 year old fallow; Bw, Beechwood).

Species composition at the study sites was very different (Fig. 4). At the arable field five species were found. However, *A. nitidus* and *S. crinita* were found only once (adult females in both cases) and *C. caeruleocinctus*, in very small numbers (adult male, adult female and a specimen of stage 3). It is doubtful therefore, if these species formed autochthonous populations on the wheat field. Two species (*P. inconstans* and *B. guttulatus*) were found frequently and different stages were present.

At the 4 year old fallow a total of 10 species was found (Fig. 4). Except for *U. foetidus* juveniles were found, indicating that almost all of these species had reproduced on that site. At the 11 year old fallow 11 species were present. From each of these species juveniles were found

Source : MNHN, Paris

indicating that these species formed autochthonous populations. In comparison to the 4 year old fallow a considerably higher ratio of specimens older than 5 years was present at the 11 year old fallow, particularly for *A. nitidus* and *C. caeruleocinctus*. At the ca 50 year old fallow only five species were present. Only one specimen of *C. londinensis* in stage 6 was found and it remains unclear if this species was able to reproduce on this site. In the beechwood six species were present, adults and juveniles of each of them were found. Despite the similar number of species in the beechwood and the ca 50 year old fallow, the species composition was very different (Fig. 4).

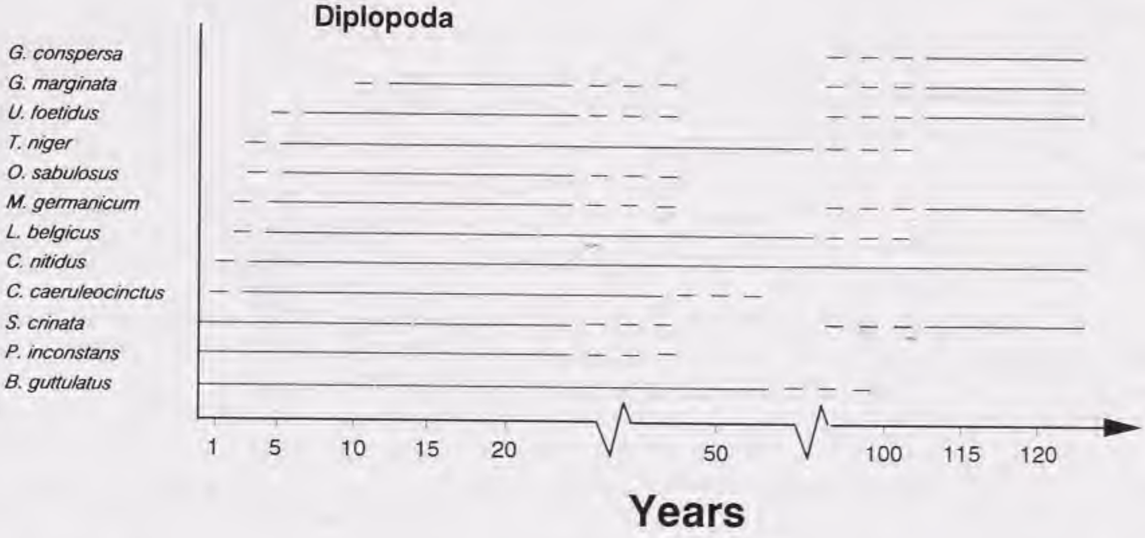


FIG. 4. — Changes in species composition of diplopods during secondary succession from a wheat field to a beechwood on limestone as indicated from the presence of diplopod species at five sites representing different stages of secondary succession.

Density and biomass

Mean density and biomass of diplopods at the arable field were almost identical in 1987 and 1988 (Table 1). Of the two dominating species, *B. guttulatus* contributed more to mean annual density and biomass than *P. inconstans* (Fig. 5). Generally, density and biomass of millipedes were high in spring and autumn and few animals were found in winter and summer.

Density and particularly biomass of diplopods at the 4 year old fallow was considerably higher than at the arable field (Fig. 6). Biomass at the 4 year old fallow peaked in autumn and only few specimens were found in winter (Table 1). *A. nitidus* dominated in density and biomass (Fig. 5) indicating that this species was the most successful colonizer during early secondary succession. Two other julid species (*C. caeruleocinctus*, *L. belgicus*) also contributed significantly to density and biomass at this site.

At the 11 year old fallow density and biomass of diplopods were generally similar to that at the 4 year old fallow, however, mean annual density at the 4 year old fallow exceeded that at the 11 year old fallow in 1987 whereas mean annual biomass at the 11 year old fallow exceeded considerably that at the 4 year old fallow in 1988 (Table 1). Similar to the 4 year old fallow, *A. nitidus* dominated in density at the 11 year old fallow (Fig. 5). *A. nitidus* and *C. caeruleocinctus* also contributed significantly to biomass in the latter, but the larger julid species *O. sabulosus* dominated, despite its low numbers. As in the 4 year old fallow biomass of the millipedes usually increased during the year and peaked in autumn.

Source : MNHN, Paris

TABLE 1. — Changes in density and biomass of diplopods at five sites representing different stages of a secondary succession from October 1986 to October 1988. ND = not determined.

Density (ind/m2)										Mean	
	10/86	1/87	4/87	7/87	10/87	1/88	4/88	7/88	10/88	1987	1988
Field	88	4	112	4	49	14	49	11	77	42	38
First fallow	95	46	98	137	343	32	126	70	179	156	102
Second fallow	270	63	84	95	165	70	130	53	182	102	109
Third fallow	ND	ND	ND	ND	242	0	28	18	81	ND	32
BeechWood	147	46	63	49	116	28	39	77	88	68	58
Biomass (mg dry mass/m2)										Mean	
Field	127	8	172	5	80	17	105	19	108	66	62
First fallow	1541	77	612	459	1455	93	976	320	1175	651	641
Second fallow	1102	450	606	294	744	1665	947	414	1956	524	1246
Third fallow	ND	ND	ND	ND	936	0	65	76	387	ND	132
BeechWood	567	90	511	175	1560	109	108	557	434	584	302

Density and biomass of millipedes at the ca 50 year old fallow were exceptionally low and similar to the field (Fig. 6). *A. nitidus* dominated in density and biomass. *L. belgicus* and *B. guttulatus* had a similar density but *L. belgicus* contributed more to biomass.

In the beechwood the density and biomass of millipedes seems to have increased considerably in comparison to the preceeding successional stage of the ca 50 year old fallow (Fig. 6). However, in comparison to the two other fallow sites density and biomas of diplopods were considerably lower in the beechwood. In the 4, 11 and ca 50 year old fallow sites *A. nitidus* dominated in density and biomass as in the beechwood, but two other species, *M. germanicum* and *G. marginata,* which were absent or rare at preceeding successional stages contributed significantly to diplopod density and biomass in the beechwood.

Species environment correlation

The biplot of diplopod species composition and environmental variables (Fig. 7a) showed a gradient from species which dominated in the wheat field (*P. inconstans*, *B. guttulatus*) to species which occurred mainly in the beechwood (*G. marginata*, *G. conspersa*, *U. foetidus*, *M. germanicum*). Species which were most abundant at the two younger fallow sites (*C. caeruleocinctus*, *O. sabulosus*) were separated from those which dominated in the beechwood by a moisture gradient and by a gradient in the amount of litter. As shown in Figure 3, the two fallow sites had the highest amounts of litter, whereas the beechwood was the most humid site (Fig. 2). The small difference in CCA eigenvalues (first axis 0.58, second axis 0.35) and DCA eigenvalues (first axis 0.74, second axis 0.46) indicate that a substantial part of the variation in species composition is represented by the environmental variables.

The CCA joint plot of samples showed four clusters (Fig. 7b). Parallel to the positions of *B. guttulatus* and *P. inconstans* (Fig. 7a), the dominating species at the wheat field, samples taken at this site were on the far right side of the diagram (first cluster). Positions of samples from the beechwood (second cluster) and the 4 and 11 year old fallow (third cluster) corresponded to the positions of the dominating species at these sites. Positions of samples from the third fallow (fourth cluster) indicate that there was no continuous change in environmental conditions during secondary succession in respect to the diplopod community. Environmental factors representing much of the dipopod variation at this site were similar to those at the arable field. Hence, in respect to the diplopod community, the arable field was most similar to the third fallow, contrasting the floral dissimilarity of the two sites.

Source : MNHN, Paris

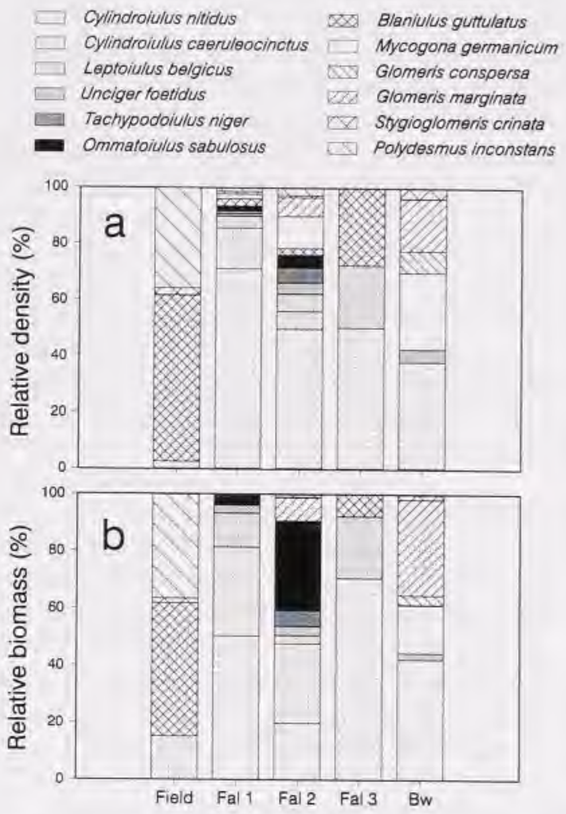


FIG. 5. — Dominance structure in density (a) and biomass (b) of diplopods at five sites representing different stages of secondary succession (legend see Fig. 3).

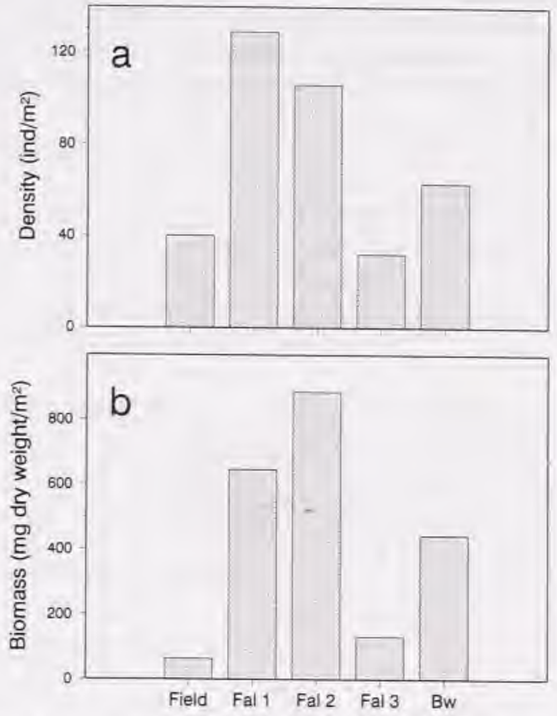


FIG. 6. — Density (a) and biomass (b) of diplopods at five sites representing different stages of secondary succession (means of 1987 and 1988 except for the third fallow which was investigated in 1988 only; legend see Fig. 3).

DISCUSSION

Succession refers to a continuous change in species composition, with time, following a perturbation. To explain the changes in species composition three hypotheses were presented (CONNELL & SLATYER, 1977): facilitation, tolerance and inhibition. The facilitation hypothesis assumes that species of early successional stages improve environmental conditions for following species (ODUM, 1969). The tolerance model assumes that species of later successional stages are more specialized; the changes in species composition being independent of the preceeding species. The inhibition model assumes that species which have colonized a distinct successional stage inhibit colonization by other species until their death. Most of these theories were developed in studies on plant communities or sessile marine animals, little attention has been paid to terrestrial animal communities.

The floral composition of the five sites investigated in the present study indicates a continuous change in plant species composition during secondary succession from the arable field to the beechwood (SCHEU, 1990b). In contrast to plants, the diplopod communities at the five sites indicate that no continuous change in millipede species occurs when arable fields are left uncultivated until formation of the climax ecosystem of a beechwood. Instead, diplopod species flourished at the 11 year old fallow and several species which occurred at this site were absent at the ca 50 year old fallow (*S. crinata*, *M. germanicum*, *U. foetidus*, *G. marginata*) but occurred again in the beechwood. Hence, the data indicate that several diplopod species become

Source : MNHN, Paris

extinct during secondary succession in an ash dominated stage and occur again in the climax ecosystem of the beechwood. TAJOVSKY (1990) also found diplopods to thrive in early stages of secondary succession. For a better understanding of changes in the diplopod community during secondary succession gradients in environmental factors should be considered.

The most extreme habitat for millipedes was the field. Cultivation presumably caused an extreme disturbance of the habitat and straw burning reduced the available food substrate. As a consequence, only species with a short life cycle (e.g. *P. inconstans*) or with a high reproductive potential (r-strategists; e.g. *P. inconstans*, *B. guttulatus*) occurred at this site. Cessation of cultivation enabled a variety of diplopod species to colonize the abandoned fields. At the 4 year old fallow at least nine species formed autochthonous populations; at the 11 year old fallow 11 reproducing species were present.

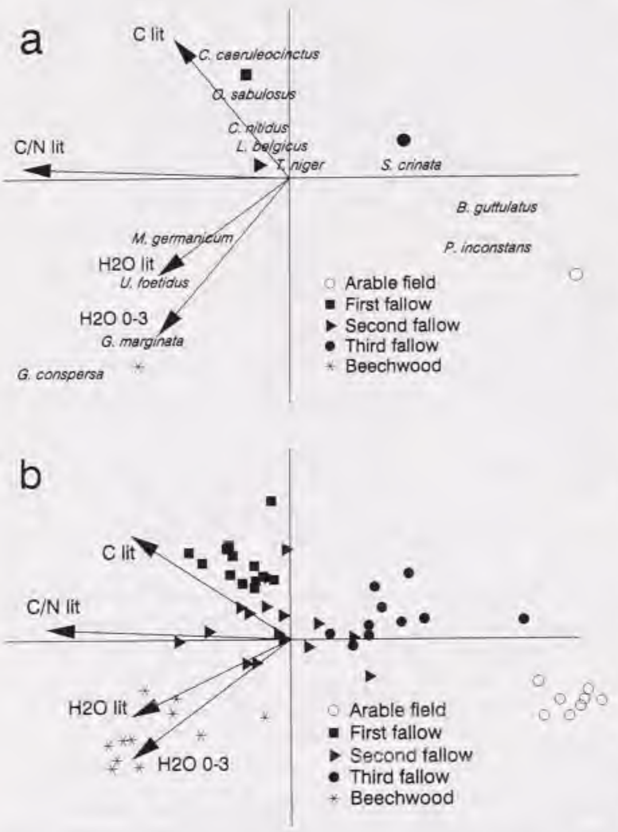


FIG. 7. — Canonical correspondence analysis biplot with environmental variables [amount of carbon in the litter layer (C lit), C/N ratio of the litter (CN lit) and gravimetric water content in the litter layer (H2O lit) and in 0-3 cm soil depth (H2O 0-3)] represented by arrows; (a) ordination of the composition of the diplopod community from five sites representing different stages of secondary succession with centroids of the five sites; (b) ordination of samples taken at the five sites (data from 1988; for details see text).

One of the most important factors responsible for the thriving of diplopods at the 4 and 11 year old fallow sites was presumably the presence of a litter layer throughout the year. Litter material may have served as food substrate, but the presence of a litter layer might have also buffered temperature and moisture extremes, e.g. frost during winter and drought in summer. As indicated by CCA ordination, the occurrence of species typical of the 4 and 11 year old fallow (e.g. *C. caeruleocinctus*, *O. sabulosus*) was related to high amounts of litter at these sites. A second factor which might have been important in structuring the diplopod communities at these sites was humidity. CCA showed that the occurrence of millipede species typical of the 4 and 11 year old fallow was related to low moisture levels in litter and soil. Obviously, these species tolerate the low moisture levels which occur at these sites particularly during summer. *C. caeruleocinctus*, *O. sabulosus* and *T. niger* as well were considered to prefer warm dry habitats (e.g. HAACKER, 1968; THIELE, 1968; DUNGER & STEINMETZGER, 1981) indicating their tolerance for low humidity. Generally, the species composition and dominance structure of the diplopod community at the 11 year old fallow was similar to that of other fallow sites investigated by STRÜWE-KUSENBERG (1981). In comparison to sites of similar age, which had been restored or developed on raw soils by primary succession (DUNGER, 1968; NEUMANN, 1971), the diplopod commmunity at the 11 year old fallow resembled those of restored afforested sites.

In comparison with the younger fallow sites, and the beechwood, the ash dominated wood (ca 50 year old fallow) was an extreme habitat for millipedes. Only few species were present and the density and biomass was low, resembling that of the wheat field. Low diversity, density and

Source : MNHN, Paris

biomass of diplopods in the ash dominated wood was unexpected because it has been shown frequently that ash leaf litter is a preferred food substrate by diplopods (DUNGER, 1958, 1962; SAKWA, 1974). However, ash leaves are also known to decompose quickly. Ash leaf litter in the ca 50 year old fallow had already disappeared almost entirely by May. The litter layer during summer, until shedding of leaves in autumn, consisted mainly of small branches and twigs from the overgrown shrub layer. The woody materials were presumably of low nutritional value for diplopods and did not form a litter layer suitable for buffering extremes in temperature and moisture.

The beechwood was characterized by the absence of species typical of the open fallow sites and the arable field and by the occurrence of *G. conspersa*. In addition, *G. marginata* and *M. germanicum* were most abundant at this site. CCA indicated that the occurrence of these species was related to humid conditions. It has been frequently found that these species preferentially colonize wooded habitats, especially *G. conspersa* which is known to occur almost exclusively in moist woodlands (BEYER, 1964; THIELE, 1968; BROCKSIEPER, 1976). The colonization of more humid ecosystems by these species presumably is related to a low tolerance of dry conditions during summer.

The content of organic matter in the upper soil layers at the five study sites indicate that wood formation was accompanied by a strong increase in soil humus. It was hypothezised by SCHEU (1992) that this increase is of considerable importance for the changes in the lumbricid community during secondary succession. In contrast, results of the CCA in the present study indicate that the soil humus content is of minor importance in determining the structure of diplopod communities. Rather, the analysis emphasized the importance of the litter layer.

The biomass of diplopods in the beechwood during the investigated period of 1987 and 1988 averaged 443 mg dry mass/m^2. Variation between years in density [coefficient of variation (CV) = 11%] was considerably lower than that in biomass (CV = 45%). The biomass at the 11 year old fallow also varied considerably between 1987 and 1988 (CV = 58%), whereas the density was almost identical (CV = 1%). There was no unidirectional change in density or biomass of the diplopod communities at the study sites from 1987 to 1988. The mean annual biomass of diplopods at the 4 year old fallow and the wheat field remained at a very constant level. At the 11 year old fallow it increased considerably (+138%), whereas in the beechwood it decreased strongly (-48%). The summer in 1988 was exceptionally dry, particularly in May, but also in August (Fig. 1). Biomass data suggest that these unusually dry conditions did not have detrimental effects on the diplopod communities of the younger fallow sites and the arable field but did on that of the beechwood (density at the 4 year old fallow might also have been affected). Presumably, the diplopod community of the beechwood is more susceptible to drought, despite the buffering capacity of the canopy of trees and the presence of a litter layer throughout the year. In a six year investigation SPRENGEL (1986) also concluded that dry summers adversely affected density and biomass of millipedes at the beechwood, particularly in autumn.

In comparison to other woodlands, the density and biomass of diplopods at the beechwood was in an approximatly central position (DUNGER, 1958; BLOWER, 1979; GEOFFROY, 1981; MEYER *et al.*, 1984; AXELSSON *et al.*, 1984). Diplopods are considered to be important agents for litter processing and nutrient cycling in forest ecosystems. The considerably higher biomass of diplopods at the younger fallow sites indicate however, that the effect of diplopods in these ecosystems may even exceed their effect in woodlands.

REFERENCES

AXELSSON, B., LOHM, U. & PERSSON, T., 1984. — Enchytraeids, lumbricids and soil arthropods in a northern deciduous woodland: A quantitative study. *Holarctic Ecol.*, **7** : 91-103.

BEYER, R., 1964. — Faunistisch-ökologische Untersuchungen an Landisopoden. *Zool. Jb. Syst.*, **91** : 341-402.

BLOWER, J. G., 1979. — The millipede fauna of two British limestone woods. *In*: M. CAMATINI, *Myriapod Biology*. London, Academic Press : 203-214.

Source : MNHN, Paris

BROCKSIEPER, J., 1976. — Isopoden und Diplopoden des Naturparks Siebengebirge. *Decheniana*, **129 :** 76-84.

CONNELL, J. H. & SLATYER, R. O., 1977. — Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.*, **111 :** 1119-1144.

DUNGER, W., 1958. — Über die Veränderung des Fallaubes im Darm von Bodentieren. *Z. Pflanzenernaehr. Dueng. Bodenkd.*, **82** : 174-193.

DUNGER, W., 1962. — Nahrungswahl bei Bodenarthropoden in produktionsbiologischer Sicht. *Verh. XI. Int. Entomol. Kongr.*, Wien 1960 : 169-173.

DUNGER, W., 1968. — Die Entwicklung der Bodenfauna auf rekultivierten Kippen und Halden des Braunkohletagebaus. *Abhandl. Ber. Naturkundemuseum Görlitz*, **43** : 1-256.

DUNGER, W. & STEINMETZGER, K., 1981. — Ökologische Untersuchungen an Diplopoden einer Rasen-Wald-Catena im Thüringer Kalkgebiet. *Zool. Jb. Syst.*, **108** : 519-553.

DUNGER, W., VOIGTLÄNDER, K., 1990. — Succession of Myriapoda in primary colonization of reclaimed land. *In*: A. MINELLI, *Proceedings 7th Intern. Congr. Myriapodology*. Leiden, Brill : 219-227.

GEOFFROY, J. J., 1981. — Etude d'un écosystème forestier mixte V. Traits généraux du peuplement de diplopodes édaphiques. *Rev. Ecol. Biol. Sol*, **18** : 357-372.

HAACKER, U., 1968. — Deskriptive, vergleichende und experimentelle Untersuchungen zur Autökologie rhein-mainischer Diplopoden. *Oecologia*, **1** : 87-129.

HERBKE, G., 1962. — Untersuchungen über das Vorkommen von Tausendfüßern in landwirtschaftlich genutzten Böden des Dauerdüngungsversuches auf Dikopfshof. *Monogr. Angew. Entomol.*, **18** : 13-42.

KEMPSON, D., LLOYD, M. & GHELARDI, R., 1963. — A new extractor for woodland litter. *Pedobiologia*, **3**: 1-21.

KLINGER, K., 1992. — Diplopods and chilopods of conventional and alternative (biodynamic) fields in Hesse (FRG). *Ber. nat.-med. Verein Innsbruck*, **Suppl. 10** : 243-250.

MEYER, E., SCHWARZENBERGER, J., STARK, G. & WECHSELBERGER, G., 1984. — Bestand und jahreszeitliche Dynamik der Bodenfauna in einem Eichenmischwald (Tirol, Österreich). *Pedobiologia*, **27** : 115-132.

NEUMANN, U., 1971. — Die Sukzession der Bodenfauna (Carabidae, Coleoptera; Diplopoda und Isopoda) in den forstlich rekultivierten Gebieten des Rheinischen Braunkohlereviers. *Pedobiologia*, **11** : 193-226.

ODUM, E. P., 1969. — The strategy of ecosystem development. *Science*, **164** : 262-270.

PETERS, D., 1984. — Faunistische und ökologische Untersuchungen der Lumbriciden, Diplopoden und Chilopoden auf verschieden bewirtschafteten Flächen der Niederrheinischen Tiefebene. Ph D Thesis, Bonn, Germany.

SAKWA, W. N., 1974. — A consideration of the chemical basis of food preference in millipedes. *Symp. Zool. Soc. London*, **32** : 329-346.

SCHAUERMANN, J., 1982. — Verbesserte Extraktion der terrestrischen Bodenfauna im Vielfachgerät modifiziert nach Kempson und Macfadyen. *Arbeitsberichte SFB*, **135** (1) : 39-45.

SCHAEFER, M., 1991. — The animal community: diversity and resources. *In*: E. RÖHRIG & B. ULRICH, *Temperate deciduous forests. Ecosystems of the world 7*. Amsterdam, Elsevier : 51-120.

SCHEU, S., 1990a. — Changes in microbial nutrient status during secondary succession and its modification by earthworms. *Oecologia*, **84** : 351-358.

SCHEU, S., 1990b. — Die saprophage Makrofauna (Diplopoda, Isopoda und Lumbricidae) in Lebensräumen auf Kalkgestein: Sukzession und Stoffumsatz. *Berichte des Forschungszentrums Waldökosysteme*. **A 57** : 1-302.

SCHEU, S., 1992. — Changes in the lumbricid coenosis during secondary succession from a wheat field to a beechwood on limestone. *Soil Biol. Biochem.*, **12** : 1641-1646.

SPRENGEL, T., 1986. — Die Doppelfüßer (Diplopoda) eines Kalkbuchenwaldes und ihre Funktion beim Abbau der Laubstreu. Ph D Thesis, Göttingen, Germany.

SCHULZ, E., 1992. — Die Milbenfauna (Acari: Mesostigmata und Cryptostigmata) in Lebensräumen auf Kalkgestein: Populationsökologie, Sukzession und Beziehungen zum Lebensraum. *Berichte des Forschungszentrums Waldökosysteme*, **A79** : 1-245.

STRÜWE-KUSENBERG, R., 1981. — Sukzession und trophische Struktur der Bodenfauna von Brachflächen. *Pedobiologia*, **21** : 132-141.

TAJOVSKY, K., 1990. — Diplopoda in a secondary soil succession row. *In*: A. MINELLI, *Proceedings 7th Intern. Congr. Myriapodology*. Leiden, Brill : 229-234.

TER BRAAK, C. J. F., 1988. — CANOCO - A FORTRAN programm for canonical community analysis by [partial] [detrended] [canonical] correspondence analysis, principle component analysis and redundancy analysis. *Technical report, TNO Inst.*, The Netherlands, Wageningen.

THIELE, H. U., 1968. — Die Diplopoden des Rheinlandes. *Decheniana*, **120 :** 343-366.

Source : MNHN, Paris

Centipedes from Italian Agroecosystems and their Possible Value as Pest Control Agents

Marzio ZAPPAROLI

Dipartimento di Protezione delle Piante, Università della Tuscia, 01100 Viterbo, Italy

ABSTRACT

The centipede communities of agroecosytems (vineyard, hazel-grove, olive-grove, chestnut-grove) and woodland stands (*Castanea sativa* coppiced wood, *Quercus cerris* woods) in Central Italy were studied in 1984-1991 by pitfall-trapping for one year in each site. Nineteen species were collected. In the agroecosystems the number of species ranges from 2 (vineyard) to 7 (hazel-grove) whereas in oak woods 7 to 10 species were collected. *Lithobius lapidicola* Meinert and *L. forficatus* (Linné) are the most common species in the agroecosystems. An attempt to assess the possible value of this group as pest control agent is discussed.

RÉSUMÉ

Les chilopodes d'agroécosystèmes d'Italie et leur valeur possible en tant qu'agents contrôlant les ravageurs.

Des recherches ont été menées sur des peuplements de chilopodes dans des agroécosystèmes (vignes, bosquets de noisetiers, oliveraies, châtaigneraies) et des sites forestiers (taillis de châtaigniers, *Castanea sativa*, forêts de chênes, *Quercus cerris*) du centre de l'Italie. Les études ont été réalisées de 1984 à 1991 à l'aide de pièges d'interception durant un an sur chaque site. 19 espèces ont été récoltées. Dans les agroécosystèmes, le nombre des espèces varie de 2 (vignes) à 7 (noisetiers) alors que dans les forêts de chênes, on trouve de 7 à 10 espèces. *Lithobius lapidicola* Meinert et *Lithobius forficatus* (Linné) sont les espèces les plus communes dans les agroécosystèmes. Une tentative d'accorder à ces groupes une valeur d'agent de contrôle des ravageurs est discutée.

INTRODUCTION

The centipede communities of Italian agroecosystems are little known and the few data available are mostly synthetized in MINELLI & IOVANE (1987). Other informations are in DACCORDI & ZANETTI (1987) on NE Italy vineyard, PAOLETTI (1988) on NE Italy maize monocultures, and ZAPPAROLI & TREMATERRA (1993) on N Italy apple orchads. Data concerning chilopods as a component of the soil community are in PAOLETTI (1980, 1988), on NE Italy maize agroecosystems, JONA LASINIO & ZAPPAROLI (1993) and TESTA & ZAPPAROLI (1994), on olive-grove and on hazelnut-grove in Central Italy.

The aim of this paper is (i) to describe the centipede communities in some agroecosystems of Central Italy, (ii) to verify the influence of the agricultural and sylvicultural activities on the qualitative composition of such communities and (iii) to assess the possible role of these polyphagous predators as pest control agent in integrated control programs.

ZAPPAROLI, M., 1996. — Centipedes from italian agroecosystems and their possible value as pest control agents. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 657-662. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

SAMPLING SITES AND METHODS

Sampling sites

Nine sites have been sampled in different localities of the Viterbo province, Latium, Central Italy: sites 1-7 are agroecosystems, representative of the predominant cultivations of the area, sites 8-9 are natural or seminatural stands, representative of the local forest vegetation potentially occurring at the same altitudinal level. The main characteristics of each site are summarized below :

1) Bassano in Teverina, 300 m a.s.l., a 15 year old vineyard, 5 ha, E exposure, bordering on open cultivated fields. Agronomic practices: chemical manures in March, May; fungicide treatments all over the cultural cycle, cultivations in spring and summer, no insecticide and herbicide treatment.

2) Caprarola, Mt. Venere, 500 m a.s.l., a 25-30 year old hazel-grove, 4 ha, SE exposure, bordering on broadleaved mixed woods and hazel-groves (see also TESTA & ZAPPAROLI, 1994). Agronomic practices: chemical manures in February, cultivations in April, May, August, insecticide treatments (Endosulfan 100 g/1000 l H_2O) in May, June, July, herbicide treatments (Glyphosate) in July, September.

3) Soriano al Cimino, St. Eutizio, 350 m a.s.l., a 20 year old hazel-grove, 3 ha, SE exposition, bordering on hazel-groves (see also TESTA & ZAPPAROLI, 1994). Agronomic practices: chemical manures in February, cultivations in April, May, June, July, August, no insecticide and herbicide treatments.

4) Canino, 120 m a.s.l., a 35-40 year old olive-grove, 4 ha, W exposure, bordering on open cultivated and grazed areas (see also JONA LASINIO & ZAPPAROLI, 1993). No agronomic practices.

5) Soriano al Cimino, St. Eutizio, 350 m a.s.l., chestnut-grove, 1 ha, W exposure, bordering on chestnut-groves and hazel-groves. Agronomic practices: cultivations in May, September, no insecticide and herbicide treatments.

6) Canepina, 650 m a.s.l., chestnut-grove, 4 ha, SE exposure, bordering on chestnut-groves. Agronomic practices: cultivations in May and September, no insecticide and herbicide treatements.

7) Caprarola, Poggio Nibbio, 550 m a.s.l., *Castanea sativa* coppiced wood, SW exposure.

8) Caprarola, Mt. Venere, 560 m a.s.l., *Quercus cerris* wood with *Ostrya carpinifolia* and *Acer obtusatum*, E exposure.

9) Caprarola, Poggio Nibbio, 580 m a.s.l., *Q. cerris* coppiced wood, SW exposure.

The area is marked by Mediterranean temperate climate, with a mean annual rainfall ranging from 700 to 1400 mm, max in October-November, min in July, mean annual temperature = 14.8 °C, max in July, min in December, aridity period in July/August. The Mediterranean characteristics of the climate in site 4 (Canino, olive-grove) are stronger than the other sites, according to its geographic position closer to the Thyrrenian sea coast. The geological substratum of the whole area is of volcanic origin (Pleistocenic), soils are clayey (TESTA & ZAPPAROLI, 1994).

Methods

Sampling has been carried out between 1984-1991 by pitfall trapping (see JONA LASINIO & ZAPPAROLI, 1993). Six traps with a 4% solution of formaldehyde in vinegar are positioned in each site for one year. Traps have been located at about 10 m one from the other along one or two rows, generally at the bases of trees, and emptied monthly. Because of limitations in the use of pitfall traps, especially for Scolopendromorpha and Geophilomorpha (ZAPPAROLI, 1992), the results will be discussed mainly qualitatively. The faunistic similarity among the sampling sites has been calculated using the JACCARD (1908) index; the hierarchic classification of the sites was undertaken using the average linkage clustering method (UPGMA).

RESULTS

Nineteen species of centipedes were collected in the sampling sites with a total of 148 specimens (Table 1). More in detail, 14 species were collected in agroecosystems (sites 1-6), 12 species in the *Quercus cerris* and coppiced *Castanea sativa* stands (sites 7-9). In the agroecosystems the number of species ranges from 2 (site 1, vineyard) to 7 (site 3, hazel-grove), whereas in oak woods 7 (site 9) to 9 (site 8) species were recorded.

A clustering of the nine sampling sites according to the similarities of their centipede fauna (cophenetic correlation index = 0.82) is shown in Figure 1. Cutting the dendrogram at low similarity level (S = 0.20) results in three clusters.

The first cluster groups vineyard and hazel-grove agroecosystems. Euryecious species are generally predominant in these habitats. *L. lapidicola* and *L. forficatus* are the most common centipedes. These species were present in the sampled woodlands as well, but the number of individuals recorded there was lower. Woodland species such as *Cryptops anomalans*, *L. acuminatus*, *L. calcaratus*, *L. castaneus* and *L. tylopus* were represented in hazel-grove as well but infrequent.

Source : MNHN, Paris

TABLE 1. — Centipedes collected in sites sampled (number of ind.). 1 = Bassano in Teverina, vineyard; 2 = Mt. Venere, hazel-grove; 3 = St. Eutizio, hazel-grove; 4 = Canino, olive grove; 5 = St. Eutizo, chestnut-grove; 6 = Canepina, chestnut-grove; 7 = Poggio Nibbio, *Castanea sativa* coppiced wood; 8 = Mt. Venere, *Quercus cerris* wood; 9 = Poggio Nibbio, *Q. cerris* wood. H = habitat preference : e = euryecious species, w = woodland species. C = chorotype : eur = European, sie = Sibiric-european, med = Mediterranean, tem = Turanic-european-mediterranean, wmd = W-Mediterranean.

species / sites	1	2	3	4	5	6	7	8	9	H	C
Himantarium gabrielis (Linné)	-	-	-	1	-	-	-	-	-	e	med
Henia vesuviana (Newport)	-	-	-	-	-	-	2	1	-	w	seu
Schendyla nemorensis (C. L. Koch)	-	-	-	-	1	-	-	1	-	w	eur
Geophilus flavus (De Geer)	-	-	-	-	-	-	-	2	-	e	sie
G. linearis C. L. Koch	-	-	1	-	-	-	-	-	-	e	sie
Pachymerium ferrugineum (C. L. Koch)	-	-	-	-	-	-	-	1	-	e	tem
Strigamia crassipes (C. L. Koch)	-	-	-	-	-	-	-	2	1	w	eur
Cryptops anomalans Newport	-	-	1	-	-	-	-	-	-	w	eur
C. hortensis Leach	-	-	-	-	2	-	-	-	-	e	eur
C. parisi Brölemann	-	-	-	-	3	1	1	2	2	w	eur
Eupolybothrus fasciatus (Newport)	-	-	-	3	-	-	1	-	6	w	seu
E. nudicornis (Gervais)	-	-	-	-	-	-	-	1	1	w	wmd
Lithobius acuminatus Brölemann	-	1	1	-	-	1	-	-	-	w	eur
L. calcaratus C. L. Koch	-	1	1	-	-	1	-	-	-	w	eur
L. castaneus Newport	-	-	1	-	-	-	1	2	2	w	seu
L. forficatus (Linné)	8	12	20	-	1	-	3	1	2	e	eur
L. lapidicola Meinert	2	4	8	-	-	-	-	-	-	e	eur
L. romanus Meinert	-	-	-	2	-	-	-	-	-	w	seu
L. tylopus Latzel	-	3	-	18	2	4	2	1	5	w	seu
tot species (19)	2	5	7	4	6	3	7	9	8		
tot specimens (148)	10	21	33	24	10	6	11	13	20		
euriecious spp. %	100	40	42.8	25	33.3	0	14.3	33.4	12.5	36.8	
woodland spp. %	0	60	57.2	75	66.6	100	85.7	66.6	87.5	63.2	

The second cluster groups together chestnut-groves and wood-land sites. The centipede community recorded in these sites is mostly represented by common woodland species of the broadleaved Central Italy woods, such as *Henia vesuviana*, *Cryptops parisi*, *Eupolybothrus fasciatus*, *Lithobius castaneus* and *L. tylopus*. Other woodland species, such as *Strigamia crassipes* and *E. nudicornis*, are present only in the two *Q. cerris* sampled sites. Anthropophilus or euryecious species, such as *Geophilus flavus*, *Pachymerium ferrugineum* and *L. forficatus*, are also present in the sampled *Q. cerris* and coppiced *C. sativa* woods.

The third cluster is only represented by the olive-grove site. The centipede community is mainly represented here by woodland species, of which *L. tylopus* is the most abundant.

The centipede communities of the sampled agroecosystems seem to be well related to the whole centipede community of the submediterranean-submontane belt of Central Italy, at least in the general features.

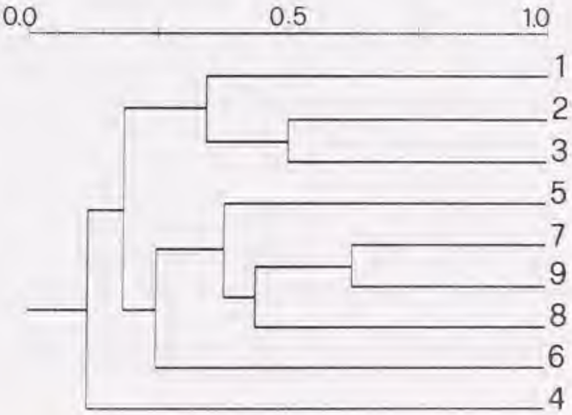


FIG. 1. — Dendrogram of hierarchical classification of the nine sampling sites. See Table 1 for abbreviations.

Source : MNHN, Paris

The anthropic impact on the pre-existent communities seems to be low, especially in chestnut-groves and hazel-groves where some woodland species are represented and a faunistic exchange between the adjacent forest habitats is probably occurring. The lower number of species generally recorded in the agroecosystems, as compared with woodlands, is probably related to the occurence of agronomic pratices, especially of the cultivations. The high frequency of these may induce changes of some soil microconditions, such as humidity degree and litter structure, and changes in community structure may be induced (TESTA & ZAPPAROLI, 1994).

It is of some interest to verify the potential value of centipedes in the control of phytophagous insects partially developing in soil, such as Coleoptera, Diptera and Lepidoptera, in agroecosystems where the stucture of vegetation is similar to that of the forest habitats (ZAPPAROLI & TREMATERRA, 1993). This potential function has already been pointed out for other major polyphagous predator Arthropoda inhabiting open European agroecosystems (cereals, arable field, etc.), such as Aranea, Coleoptera Carabidae and Staphylinidae (BRIGNOLI, 1983; SUNDERLAND & CHAMBERS, 1983). Besides, among Chilopoda especially Lithobiidae have been pointed out as active soil-inhabiting predators in many European and Mediterranean agroecosystems (SUNDERLAND, 1975; CAUSSE, 1976; TEMERAK, 1983).

Among the agroecosystems of the study area, centipedes are generally well represented in species and numbers especially in hazel- and chestnut-groves which represent the most important local cultivations. In hazel-groves, key pest in Central Italy is *Balaninus nucum* L. (Coleoptera Curculionidae), this species completes one generation every 2-5 years and spends part of the biological cycle in soil as mature larval stadium, pupa or adult as well, from June-July to the end of spring, 15-50 cm deep (PUCCI, 1992).

According to the results of the sampling discussed above, the activity peak observed in the centipede communities of the study area matches well with the phenology of the mature larvae and pupae of *B. nucum* (Table 2). Moreover, in hazel-grove centipede community, the most important species from the quantitative point of view is *L. forficatus*, which seems to be active all over the year with a peak in July-September (Table 2). This species is well known as a pioneer in artificial and disturbed European habitats and it also frequently occurs in Italian agroecosystems (MINELLI & IOVANE, 1987; PAOLETTI, 1988; ZAPPAROLI & TREMATERRA, 1993). *L. forficatus* usually preys on a large spectrum of small soft-bodied invertebrates species, mainly arthropods and annelids (LEWIS, 1981) it has been already recorded as an important predator of pupae of *Rhagoletis pomonella* Walsh (Diptera Tephirtidae), a key pest in the Canadian apple ochards (MONTEITH, 1975, 1976).

TABLE 2. — Number of individuals of centipedes (in brakets *L. forficatus*) collected monthly in the sites sampled. 1 = Bassano in Teverina, vineyard; 2 = Mt. Venere, hazel-grove; 3 = St. Eutizio, hazel-grove; 4 = Canino, olive grove; 5 = St. Eutizo, chestnut-grove; 6 = Canepina, chestnut-grove; 7 = Poggio Nibbio, *Castanea sativa* coppiced wood; 8 = Mt. Venere, *Quercus cerris* wood; 9 = Poggio Nibbio, *Q. cerris* wood.

sites/months	J	F	M	A	M	J	J-A	S	O	N	D
1	-	-	-	2(1)	1(1)	2(2)	2(2)	1(1)	1(-)	1(1)	-
2	-	-	3(-)	-	-	4(2)	6(6)	5(3)	2(1)	-	1(-)
3	-	-	1(-)	7(3)	4(4)	1(1)	5(2)	9(5)	2(2)	2(2)	2(1)
4	2(-)	3(-)	1(-)	-	-	2(-)	8(-)	5(-)	1(-)	2(-)	-
5	1(-)	2(1)	3(-)	2(-)	1(-)	-	-	-	-	1(-)	-
6	2(-)	-	-	1(-)	-	-	-	-	3(-)	2(-)	-
7	1(-)	2(-)	-	-	-	1(1)	2(-)	-	-	3(2)	-
8	1(1)	1(-)	-	-	2(-)	1(-)	3(-)	1(-)	1(-)	2(1)	2(-)
9	1(1)	2(-)	-	2(-)	2(1)	1(-)	8(-)	1(-)	1(-)	-	1(-)

Source : MNHN, Paris

CONCLUSION

Tentatively, we hypothesize that *L. forficatus* can play an important role among predators in the biocontrol of *B. nucum* in Central Italy hazel-groves.

More evidence is necessary however, to support the possible role of Chilopoda as pest control in agroecosystems. As SUNDERLAND & CHAMBERS (1983) suggest, many problems will have to be solved in order to assess the potential value of such predators: field and laboratory trials on which species are preyed on and the ability to prey are needed together with informations on the predator's behaviour, ecology and density during the years in different sites and under different farming conditions.

On the other hand, as stated by WATERHOUSE (1969), the individual number of centipedes in the field may be too low to give an adequate control of pest. As pointed out by several European studies (see SUNDERLAND & CHAMBERS, 1982; THOMAS *et al.*, 1992), the activity of these predators should therefore be useful in integrated pest control programs in cooperation with other polyphagous Arthropoda, specialist parasites and predators, under more favourable farming conditions such as reduced inputs of pesticides, reduced rates of cultivations and increased and conserved structural diversity within the agroecosystems.

ACKNOWLEDGEMENTS

This research has been partly supported by grant of the Italian Ministero della Ricerca Scientifica e Tecnologica.

REFERENCES

BRIGNOLI, P. M., 1983. — I ragni quali predatori di insetti: il loro potenziale ruolo negli agroecosistemi (Araneae). *In*: *Atti XIII Congr. Naz. It. Ent., Sestriere*. Torino : 591-597.

CAUSSE, R., 1976. — Etude de la localisation et de la mortalité hivernale des larves de *Laspeyresia pomonella* L. (Lepidoptera, Tortricidae) en vergers modernes de pommiers de la basse Vallée du Rhône. *Ann. Zool. Ecol. Anim.*, **8** : 83-101.

DACCORDI, M. & ZANETTI, A., 1987. — Catture con trappole a caduta in un vigneto nella Provincia di Verona. *Quad. Az. Agraria Sper. Villafranca*, **3** : 1-44.

JACCARD, P., 1908. — Nouvelles recherches sur la distribution florale. *Bull. Soc. Vaud. Sci. Nat.*, **44** : 223-270.

JONA LASINIO, P. & ZAPPAROLI, M., (1993). — First data on the soil Arthropod community in an olive grove in Central Italy. *In* : M. PAOLETTI, W. FOISSNER & D. COLEMAN, *Soil Biota, Nutrient Cycling and Farming Systems. Proc. Int. Symp. "Agroecology and conservation issues in temperate and tropical regions"*, Chelsea, USA, Lewis Publisher : 113-121.

LEWIS, J. G. E., 1981. — *The biology of centipedes*. Cambridge, Cambridge University Press, 476 pp.

MINELLI, A. & IOVANE, E., 1987. — Habitat preferences and taxocenoses of Italian centipedes (Chilopoda). *Boll. Mus. civ. St. nat. Venezia*, **37** : 7-34.

MONTEITH, L. G., 1975. — Laboratory feeding studies on potential predators of the apple maggot *Rhagoletis pomonella* (Diptera Tephritidae) in Ontario. *Proc. entom. Soc. Ontario*, **106** : 28-33.

MONTEITH, L. G., 1976. — Field studies on potential predators of the apple maggot *Rhagoletis pomonella* (Diptera Tephritidae) in Ontario. *Proc. entom. Soc. Ontario*, **107** : 23-30.

PAOLETTI, M. G., 1980. — L'agroecosistema a mais nella pianura veneta con raffronti all'ambiente planiziale forestale. Alcune valutazioni qualitative e quantitative sugli invertebrati del suolo. *In*: *Atti I Congr. naz. s. It. E.* : 359-369.

PAOLETTI, M. G., 1988. — Soil invertebrates in cultived and uncultivated soils in Northeastern Italy. *Redia*, **71** : 501-563.

PUCCI, C., 1992. — Studies on population dynamics of *Balaninus nucum* L. (Col. Curculionidae) noxoius to the hazel (*Corylus avellana* L.) in Northern Latium (Central Italy). *J. Appl. Ent.*, **114** : 5-16.

SUNDERLAND, K. D., 1975. — The diet of some predatory arthropods in cereal crops. *J. Appl. Ecol.*, **12** : 507-515.

SUNDERLAND, K. D. & CHAMBERS, R. J., 1983. — Invertebrate polyphagous predators as pest control agents: some criteria methods. *In* : R. CAVALLORO, *Aphid antagonists, Proc. Meeting ZC Experts' Group*, Rotterdam, Balkema : 100-108.

TEMERAK, S. A., 1983. — A preliminary survey on the soil-inhabiting predaceous arthropods associated with pupae of the large sucarcane borer, *Sesamia cretica* in sorghum field. *Bull. Soc. ent. Egypte*, **62** : 251-255.

Source : MNHN, Paris

TESTA, G. & ZAPPAROLI, M., 1994. — First data on soil Arthropod communities of hazel groves in Central Italy. [*In*: *Proc. III ISHS Int. Congress Hazelnut, Alba, Italy*]. *Acta Horticulturae*, **351** : 631-637.

THOMAS, M. B., WRATTEN, S. D. & SOTHERTON, N. W., 1992. — Creation of "island" habitats in farmland to manipulate populations of beneficial arthropods: predator densities and species composition. *J. Appl. Ecology*, **29** : 524-531.

WATERHOUSE, J. S., 1969. — An evaluation of a new predaceous centipede *Lamyctes* sp., on the garden symphylan *Scutigerella immaculata*. *Can. Entom.*, **101** : 1081-1083.

ZAPPAROLI M., 1992. — Preliminary data on centipede communities of *Quercetea ilicis* and *Fagetalia sylvaticae* in Central Italy. *Ber. nat.-med. Verein Innsbruck*, **suppl. 10** : 197-204.

ZAPPAROLI, M. & TREMATERRA, P., 1993. — Chilopodi nei meleti della Valtellina. *Boll. Zool. agr. Bachic.* (II), **25** : 41-48.

Source : MNHN, Paris

Author Index / Index des auteurs

ABROUS-KHERBOUCHE, Ourida ... 175
ADIS, Joachim ... 523, 607
ADOLPHE, Jean-Pierre ... 555
AGUILAR, Franklin ... 493
ANDREJKO, Mariola ... 431
BANO, Kubra ... 73, 561
BARBER, Antony D. ... 243
BARNETT, Mandy ... 331
BARRIENTOS, Zaidett ... 493
BOUZERNA, Noureddine ... 365
BRANQUART, Etienne ... 485
CANCELA DA FONSECA, Jorge P. ... 577
CÉLÉRIER, Marie-Louise ... 533
CEUCA, Traian ... 61
COMPÈRE, Philippe ... 395
CONDÉ, Bruno ... 127
DAAS, Tarek ... 365
DANGERFIELD, John Mark ... 565, 617
DAVID, Jean-François ... 461, 627
DE MORAIS, José Wellington ... 607
DEFIZE, Stéphane ... 395
DEMANGE, Jean-Marie ... 21
DESCAMPS, Michel ... 365, 385, 391
DOHLE, Wolfgang ... 371
DOMINGUEZ RODRIGUEZ, Maria Teresa ... 137
EL AISSAOUI, Hsaïn ... 555
ENGHOFF, Henrik ... 313
FABRE, Marie-Chantal ... 385, 391
FISCHER, Elisabeth ... 451
FUSCO, Giuseppe ... 351
GARCIA RUIZ, Andrès ... 205, 347
GASPAR, Charles ... 485
GEOFFROY, Jean-Jacques ... 13, 269, 533
GÉRARD, Sylvie ... 391
GOFFINET, Gerhard ... 395
GOLOVATCH, Sergei Illich ... 163, 265, 523
GREVEN, Hartmut ... 403
HAMANN, Susanne ... 523
HILL, Trevor J. ... 441
HOPKIN, Stephen P. ... 25
ISHII, Kiyoshi ... 101
JAMAULT-NAVARRO, Catherine ... 385
JAROSZ, Jan ... 431
JEANSON, Colette ... 555
JEDRYCZKOWSKI, Wojcieh B. ... 209
JONES, Richard E. ... 243
KANIA, Grzegorz ... 431
KIME, Richard Desmond ... 257
KORSÓS, Zoltàn ... 35
KOS, Ivan ... 635
KRAUS, Margarete ... 283
KRAUS, Otto ... 283
LESNIEWSKA, Malgorzata ... 221
LEWIS, John G. E. ... 441
MAHSBERG, Dieter ... 585
MARSONER, Peter ... 451
MARTENS, Jochen ... 163
MAURIÈS, Jean-Paul ... 81
MATEOS, Eduardo ... 187
MATIC, Zachiu ... 225
MESIBOV, Robert ... 139, 341
MEYER, Erwin ... 451
MEZIANE, Leïla ... 577
MINELLI, Alessandro ... 351
MIQUEL, Maria Carme ... 359
MONGE-NAJERA, Juliàn ... 493
NEGREA, Stefan ... 225
NEGRISOLO, Enrico ... 351
NEVERMANN, Lutz ... 421
NGUYEN DUY - JACQUEMIN, Monique ... 113
PASS, Günther ... 291
PEDROLI-CHRISTEN, Ariane ... 45, 53, 281
PEREIRA, Luis Alberto ... 79
PRUNESCU, Carol Constantin ... 299, 341, 437
PRUNESCU, Paula ... 437
REVAULT, Pascal ... 495
RIBAROV, Goergi ... 235
ROSENBERG, Jörg ... 403
RUHBERG, Hilke ... 139
SAHLI, François ... 373, 587
SANTIBANEZ, Francisco J. ... 205, 347
SCHELLER, Ulf ... 607
SCHEU, Stefan ... 647
SCHILEYKO, Arkady A. ... 293
SCHOLL, Adolf ... 45, 53
SERRA, Antoni ... 187, 359
SHINOHARA, Keizaburo ... 341
SPELDA, Jörg ... 151
STEFANIAK, Malgorzata ... 431
STRIGANOVA, Bella R. ... 515
SUSTR, Vladimir ... 473
TABACARU, Ionel ... 67
TADLER, Andreas ... 327
TAJOVSKY, Karel ... 509
TAMURA, Hiroshi ... 101
TELFORD, Steven R. ... 331, 565, 617
VANNIER, Guy ... 461
VICENTE, Maria Cristina ... 187
VOIGTLÄNDER, Karin ... 501
WAKLEY, Gavin E. ... 441
WANG, Daqing ... 81, 307
WEYDA, Frantizek ... 483
WYTWER, Jolanta ... 213
XYLANDER, Willi E. R. ... 411, 421
ZALESSKAYA, Nadezhda ... 265
ZAPPAROLI, Marzio ... 599, 657
ZULKA, Klaus Peter ... 477

Source : MNHN, Paris

Source : MNHN, Paris

SYSTEMATIC INDEX

A

Adenomeris gibbosa 245, 247, 248, 249, 275
Adenomeris hispida 275
Agariogonopus acrotrifoliatus 85
Alaskobius takakuwai 91
Alipes 294, 295
Allajulus nitidus 245, 248, 258, 260, 262, 278, 374, 488, 533, 537, 545, 546, 547, 548, 549, 550, 647, 649, 650, 651, 652
Allajulus spinosus 326
Allopauropus ovalapendicis 91
Allopauropus pilosisphaerus 91
Alloporus 333, 334, 337
Alloporus uncinatus 333, 335, 337, 567, 568, 569, 570, 571, 573, 574, 575, 618, 619, 620, 621, 622, 623, 624
Alloproctus 133
Alogolykinae 74, 86
Alogolykini 75, 86
Alpiobates peyerimhoffi 277
Alpityphlus seewaldi, 154, 157
Altum 309
Altum carinatum 307, 308, 309, 310
Altum serratum 307, 308, 309, 310
Altum viriosum 307, 308, 309, 310
Amblyiulus 85
Amblyiulus barroisi 326
Amblyiulus creticus 326
Ameractis chirogon 326
Ampelodesmus 111
Ampelodesmus granulosus 102, 108
Anamastigona pulchella 276
Anaulaciulus 35, 36, 42, 167, 172, 173, 313, 318, 324
Anaulaciulus acaudatus 36, 39, 167
Anaulaciulus acutus 36, 39, 41
Anaulaciulus attemsii 36, 39
Anaulaciulus bilineatus 37, 39, 40, 42, 167
Anaulaciulus bilobus 37, 39, 41
Anaulaciulus capillatus 37, 40
Anaulaciulus ciliatus 36
Anaulaciulus cornutus 37, 39
Anaulaciulus enghoffi 37, 39
Anaulaciulus golovatchi 37, 40, 41, 42
Anaulaciulus hirosaminus 37, 39
Anaulaciulus inaequipes 37, 39, 40, 41, 42, 317, 326
Anaulaciulus kashmirensis 37, 39, 167
Anaulaciulus kiusiensis 37, 40, 41
Anaulaciulus komatsui 37, 39
Anaulaciulus koreacolus 37, 39, 42
Anaulaciulus koreanus 37, 39, 40, 41
Anaulaciulus koreanus boninensis 37
Anaulaciulus koreanus tuberculatus 37
Anaulaciulus kuritai 37, 39
Anaulaciulus longus 37, 39
Anaulaciulus nepalensis 37, 38, 39, 42, 167
Anaulaciulus niger 38, 39, 42, 167
Anaulaciulus okinawaensis 38, 39
Anaulaciulus onychophora 38, 39
Anaulaciulus otigonopus 38, 39, 41
Anaulaciulus pakistanus 38, 39, 42
Anaulaciulus paludicola 36, 38, 39, 40, 42, 85
Anaulaciulus pinetorum 38, 39
Anaulaciulus pinetorum nivalis 38
Anaulaciulus quadratus 38, 39, 41
Anaulaciulus riedeli 38, 39, 41, 42
Anaulaciulus ryugadensis 38, 40, 42
Anaulaciulus simodanus 38, 39
Anaulaciulus simplex 38, 39, 85
Anaulaciulus takakuwai 38, 39
Anaulaciulus takakuwai coloratus 38
Anaulaciulus takanoi 38, 40, 42
Anaulaciulus tibetanus 38, 39, 167
Anaulaciulus tigris 38, 39, 42
Anaulaciulus tonggosanensis 38, 39
Anaulaciulus tonginus 39, 41, 42, 85, 326
Anaulaciulus topali 39, 167
Anaulaciulus trapezoidus 39, 85
Anaulaciulus trigonalis 39
Anaulaciulus trilobus 39, 41, 85
Anaulaciulus trilobus khuuae 85
Anaulaciulus trilobus quemoyensis 85
Anaulaciulus vallicola 36, 39, 40, 85
Anaulaciulus yamashinai 39, 42
Anaulaciulus yosidanus 39, 40
Androgнathidae 84, 167, 171
Aniulus 326
Anoplodesmus 74
Anoplodesmus anthracinus 74
Anoplodesmus atopus 74
Anoplodesmus indus 74
Anoplodesmus insignis 74
Anoplodesmus saussurii 74
Anoplodesmus tanjoricus 74
Anopsobiidae 346
Anopsobiini 304, 341
Anopsxenus 122
Anopsxenus caboverdus 113, 114, 121, 122, 123, 125
Anopsxenus indicus 113, 114, 121, 122, 123, 125
Anthogona britannica 244, 245, 247, 248,
Anthogona variegata 276
Antichirogonus 75
Antichirogonus hirtus 75
Antichirogonus laevisulcatus 75
Antisoma 74
Aphelidesmus 74
Aponedyopus jeanae 87
Aponedyopus maculatus 87
Aponedyopus montanus 87
Aponedyopus reesi 87
Aprosphylosoma darceneae 326
Aprosphylosomatidae 326
Archiboreoiulus pallidus 245, 247, 248, 258, 260, 271, 277

Source : MNHN, Paris

Archiboreoiulus sollaudi 277
Archileucogeorgia 318, 326
Archilithobius carinatus 225
Archipolydesmus 180, 182, 185
Archipolydesmus osellai 190, 193
Archipolydesmus ribauti 277
Archispirostreptus tumuliporus 470
Arebius bidens 90
Arebius chengsiensis 90
Armolites 169
Armolites chulingensis 169
Armolites communicans 169
Armolites similis 169
Armolites spiniger 76, 169
Arrupinae 89
Asanada 294, 295
Asanada socotrana 448
Assamodesmus 168
Assamodesmus lindbergi 168
Atractosoma montivaga 53, 54, 55, 57, 58
Atractosoma montivaga hessei 55
Atractosoma montivagum silvaticum 54

B

Bacillozonium nodulosum 515
Ballophilinae 88
Ballophilus liber 88
Banatodesmus jeanneli 68
Baskoiulus stammeri 326
Basoncopus filiformis 326
Bhutanodesmus 169
Bhutanodesmus velatus 169
Bilingulidae 83
Bilingulus sinicus 85
Blaniulidae 326, 650
Blaniulidea 272, 277, 278
Blaniulus dollfusi 190, 193
Blaniulus guttulatus 211, 245, 246, 247, 248, 250, 258, 277, 374, 628, 647, 649, 650, 651, 652, 654
Blaniulus lichtensteini 277
Blaniulus lorifer 277
Blaniulus mayeti 277
Blaniulus orientalis 277
Blaniulus troglobius 277
Blaniulus troglodites 277
Blaniulus velatus 277
Blaniulus virei 278
Bollmania 86
Boreoiulus dollfusi 277
Boreoiulus simplex 278
Boreoiulus tenuis 211, 245, 248, 258, 278
Bothriogaster signata 238, 600, 601
Bothropolys 366
Bothropolys asperatus 90
Bothropolys crassidentatus 91
Bothropolys elongatus 366
Bothropolys imaharensis 91
Bothropolys richthofeni 91
Bothropolys shansiensis 91
Brachychaeteuma 247
Brachychaeteuma bagnalli 245, 248, 271, 276
Brachychaeteuma bradae 245, 248, 276
Brachychaeteuma cadurcensis 276
Brachychaeteuma furcatum 276
Brachychaeteuma melanops 245, 247, 248, 276
Brachychaeteuma peniculatum 276
Brachychaeteuma plumosum 276
Brachychaeteuma provinciale 276
Brachycybe lecontii 483
Brachydesmus 101
Brachydesmus exiguus 277
Brachydesmus proximus 277
Brachydesmus superus 211, 245, 246, 247, 248, 250, 258, 260, 277
Brachygeophilus truncorum 215, 219, 222, 223
Brachyiulidae 328
Brachyiulinae 36
Brachyiulini 36, 173, 317, 324, 326
Brachyiulus 314, 317, 481
Brachyiulus apfelbecki 317, 326
Brachyiulus bagnalli 328, 477, 478, 479, 480
Brachyiulus lusitanus 278
Brachyiulus pusillus 245, 248, 258, 260, 278
Brachyschendyla 639
Brachyschendyla montana 638, 639, 640, 641, 642, 643, 644, 645
Brachyschendyla varnensis 238
Broelemanneuma 273
Broelemanneuma furcatum 274, 276
Broelemanneuma gayi 274, 276
Broelemanneuma gineti 274, 276
Broelemanneuma palmatum 274, 276
Broelemanneuma pectiniger 274, 276
Buchneria cornuta 321
Buchneria sicula 321

C

Californiulus yosemitensis 326
Callipodidea 276, 307
Callipus corsicus 276
Callipus foetidissimus 276, 596
Callipus sorrentinus 276
Calostreptus 566, 572, 574
Calostreptus carinatus 567, 569, 570, 571, 573, 618, 620, 621, 622
Calyptophyllini 313, 315, 319, 320, 324, 326
Calyptophyllum digitatum 319, 326
Calyptophyllum trapezolepis 319, 326
Cambalidae 85
Cambalopsidae 168, 171
Camptogona delamarei 276
Camptogona duboscqui 276
Caspiopetalidae 86
Catamicrophyllini 315, 324
Catamicrophyllum 320
Catamicrophyllum caifanum 320, 326
Catamicrophyllum mesorientale 319, 326
Centrodesmus 102

Source : MNHN, Paris

Cephalofovea tomahmontis 148
Ceratosphys 190, 193
Ceratosphys amoena 276
Ceratosphys banyulsensis 276
Ceratosphys guttata 276
Ceratosphys nivium 276
Ceratosphys picta 276
Ceratosphys simoni 276
Ceratosphys vandeli 276
Cermatidae 32
Cermatobiidae 300, 301
Chaetechelyne 639
Chaetechelyne illyriaca 642
Chaetechelyne scheerpeltzi 638, 639
Chaetoleptophyllum 326
Chalandea 639
Chaleponcus 333, 335, 337, 338, 570, 572, 574, 623
Chaleponcus digitatus 567, 569, 570, 571, 573, 574, 619, 620, 621
Chaleponcus limbatus 333, 334, 337, 570, 571, 573, 619, 621, 622
Chamaesoma broelemanni 276
Chamberlinini 87
Chamberlinius cristatus 102
Chamberlinius haulienensis 87, 102
Chamberlinius pekuensis 87
Chamberlinius picrofasciatus 87
Chamberlinius shengmui 87
Chelodesmidea 88
Chelojulidae 326
Chelojulus sculpturatus 326
Chersastus 566
Chersastus sanguinipes 569
Chersoiulus sphinx 326
Chicobolus 411, 412, 413, 414, 415, 416, 417, 418, 434
Chilexenus 121
Chinobius chekianus 90
Chinobius chekianus tumeopes 90
Chinobius pachypedatus 90
Chinobius sachalinus 90
Chinobius sulcipes 90
Chinobius svenhedini 90
Chinosoma hodites 86
Chinosphaera maculosa 84
Chinosphaera majorina 84
Chinosphaera multidenta 84
Chondromorpha 74
Chondromorpha kaimura 75
Chondromorpha kelaarti 75
Chondromorpha kelaarti longipes 75
Chondromorpha kelaarti valparaiensis 74
Chondromorpha mammifera 74, 76
Chondromorpha severini 74
Chondromorpha severini var. robusti 74
Choneiulus palmatus 211, 245, 247, 248, 258, 278
Choneiulus subterraneus 278
Chordeuma 244, 245
Chordeuma consoranense 277
Chordeuma iluronense 277
Chordeuma inornatum 277
Chordeuma intermedium 277
Chordeuma montanum 277
Chordeuma muticum 277
Chordeuma proximum 245, 246, 248, 249, 252, 277
Chordeuma reflexum 277
Chordeuma silvestre 245, 246, 248, 258, 260, 262, 277, 488
Chordeuma trifidum 277
Chordeuma utriculosum 277
Chordeuma vasconicum 277
Chordeumatidae 650
Chordeumatidea 272 277, 489
Chordeumella 509
Chromatoiulus 318
Chromatoiulus podabrus 318, 326
Cleidogonidae 167
Clinopodes 639
Clinopodes abbreviatus 638, 639, 640, 642, 643, 644, 645
Clinopodes flavidus 222, 223, 238, 601, 602, 641, 644
Clinopodes linearis 215, 219, 222, 223, 638, 639, 641, 644
Clinopodes trebevicensis 601, 603, 638, 639, 641, 642, 643, 644, 645
Cormocephalus 294, 295
Corsicosoma legeri 276
Corsikomeris remyi 275
Corypholophus 102, 110
Cranogona dalensi 276
Cranogona delicata 276
Cranogona denticulata 276
Cranogona orientale 276
Cranogona pavida 276
Cranogona touyaensis 276
Cranogona uncinata 276
Cranogona vasconica 276
Craspedosoma 262
Craspedosoma alemannicum 258, 259, 262, 276
Craspedosoma rawlinsii 245, 247, 248, 259, 262, 276, 488, 489
Craspedosoma simile 258, 259
Craspedosoma taurinorum conforme 276
Craspedosomatidae 45
Craspedosomatidea 272, 276, 277, 489, 537
Craterostigmus 346, 437
Craterostigmus tasmanianus 305,341, 342, 346, 437,438, 439, 440
Crenatidorsus grandifoliatus 87
Crossosoma broelemanni 276
Crossosoma cavernicola 271, 276
Crossosoma mauriesi 271, 276
Crossosoma peyerimhoffi 276
Cryptocorypha 111
Cryptocorypha japonica 102, 108
Cryptocorypha spinicoronatus 88
Cryptodesmidae 71, 87, 102, 108, 110, 111, 168, 171
Cryptops 294, 295, 441, 639
Cryptops anomalans 238, 601, 602, 658, 659
Cryptops anomalans anomalans 236
Cryptops anomalans schassburgensis 236
Cryptops croaticus 238, 638
Cryptops hispanus 206, 207

Source : MNHN, Paris

Cryptops hortensis 222, 223, 238, 601, 602, 638, 640, 641, 642, 643, 644, 645, 659
Cryptops japonicus 90
Cryptops nigropictus 90
Cryptops parisi 236, 601, 638, 639, 640, 641, 642, 643, 644, 659
Cryptops parisi parisi 236
Cryptops parisi rhenanus 236
Cryptops rucneri 638
Cryptops trisulcatus 600, 601
Cryptopsidae 90, 293, 294, 295, 296, 297
Cryptopsinae 90
Ctenophilus 79
Ctenophilus amieti 79
Ctenophilus chevalieri 79
Ctenophilus corticeus 79
Ctenophilus edentulus 79
Ctenophilus magnus 79
Ctenophilus nesiotes 79
Ctenophilus nitidus 79
Ctenophilus oligopodus 79
Ctenophilus pratensis 79
Curiosoma bispinosum 76
Cutervodesmus 71
Cutervodesmus adisi 523, 524, 525, 526, 527, 528, 529, 530
Cylindroiulinae 328
Cylindroiulini 318, 321, 322, 325, 326
Cylindroiulus 212, 325, 627
Cylindroiulus bicolor 322, 326
Cylindroiulus boleti 328, 478, 479
Cylindroiulus britannicus 245, 246, 247, 248
Cylindroiulus broti 278, 322, 326, 597
Cylindroiulus caeruleocinctus 190, 193, 195, 201, 203, 211, 212, 245, 246, 247, 248, 252, 258, 259, 260, 262, 263, 278, 326, 537, 550, 627, 628, 629, 630, 647, 649, 651, 652, 654
Cylindroiulus chalandei 278
Cylindroiulus distinctus 182
Cylindroiulus frisius 211, 212
Cylindroiulus iluronensis 278
Cylindroiulus latestriatus 212, 245, 247, 248, 250, 252, 254, 258, 278, 501, 502, 503, 504, 505, 506, 507, 517
Cylindroiulus latzeli 326
Cylindroiulus laurisilvae 322, 326
Cylindroiulus limitaneus 278, 596
Cylindroiulus londinensis 245, 246, 247, 248, 250, 252, 255, 262, 278, 628, 651
Cylindroiulus nitidus 545
Cylindroiulus parisiorum 245, 247, 248, 278
Cylindroiulus perforatus 326
Cylindroiulus propinquus 326
Cylindroiulus punctatus 245, 246, 247, 248, 258, 259, 260, 278, 326, 488, 504, 505, 517, 533, 537, 544, 545, 547, 548, 549, 550
Cylindroiulus pyrenaicus 278
Cylindroiulus ruber 322 326
Cylindroiulus sagittarius 278
Cylindroiulus schubarti 278
Cylindroiulus segregatus 278
Cylindroiulus spinosus 278
Cylindroiulus truncorum 211, 245, 247, 248, 255, 257, 258
Cylindroiulus verhoeffi 278
Cylindroiulus vulnerarius 245, 247, 248, 254, 255, 278
Cyrnosoma beroni 276
Cyrnosoma coineaui 276
Cyrnosoma strasseri 276

D

Dalodesmidae 71
Dasypharkis 75
Dasypharkis rugulosa 75
Delurodesmus orientalis 88
Desmoxytes cornuta 87
Desmoxytes draco 87
Desmoxytes longispina 87
Desmoxytes minutubercula 87
Desmoxytes piceofasciata 87
Desmoxytes planata 75, 76, 87
Desmoxytes rastrituberus 87
Devillea tuberculata 277
Devonobius delta 289
Dicellophilus 639
Dicellophilus carniolensis 638, 639, 640, 641, 642, 644, 645
Dignathodon microcephalum 206, 207, 238, 240, 347, 348, 349, 600, 601
Dignathodontinae 88
Dimorphodesmus 102, 109, 111
Dinocryptops 294
Diplomaragna formosanum 86
Diplomaragnidae 86
Doderoa genuensis 275
Dolichoiulus 271, 315
Dolichoiulus tongiorgii 271, 278
Dolichoiulus vosseleri 326
Doratodesmidae 87, 102, 109, 110, 111
Doratogonus 333, 334, 337

E

Enantiulus armatus 245, 246, 248, 249, 252, 254, 278
Enantiulus dentigerus 326
Enantiulus nanus 278, 451, 452, 453, 454, 455, 456, 458, 505
Epanerchodus 107, 111
Epanerchodus eurycornutus 87
Epanerchodus mammillatus 102, 107
Epanerchodus orientalis 87, 102
Epanerchodus potanini 87
Epanerchodus shirinensis 87
Epanerchodus sphaerisetosus 87
Epanerchodus stylotarseus 87
Epanerchodus takakuwai 87
Epinannolene arborea 524
Epiperipatus biolleyi 493, 494
Esastigmatobius 304

Source : MNHN, Paris

Esastigmatobius longicornis 91
Esastigmatobius longitarsis 91, 341, 342, 346
Escaryus japonicus 88
Escaryus latzeli 88
Escaryus sachalinus 88
Escualdosoma gourbaultae 276
Ethmostigmus 294, 295, 441, 442, 444, 447, 448
Ethmostigmus trigonopodus 441, 442, 444, 447, 448
Ethopetolidae 90
Eucondylodesmus 111
Eucondylodesmus elegans 102, 109
Eudigraphis sinensis 84
Eudigraphis taiwaniensis 84
Eumastigonodesmus boncii 277
Euperipatoides leuckarti 141, 148
Euphoberia 483
Eupolybothrus 225, 226, 232, 603, 604, 639
Eupolybothrus andreevi 238
Eupolybothrus caesar 601, 602, 603, 604
Eupolybothrus elongatus 365, 366, 367, 369
Eupolybothrus fasciatus 225, 226, 229, 238, 659
Eupolybothrus grossipes 236
Eupolybothrus litoralis 225, 227, 228, 229, 232, 600, 601, 603, 604
Eupolybothrus nudicornis 659
Eupolybothrus ochraceus 238
Eupolybothrus transsylvanicus 238, 601, 602, 603, 604
Eupolybothrus tridentinus 238, 240, 639, 644
Eupolybothrus valkanovi 238
Eupolybothrus verrucosus 266, 267, 268
Eupolybothrus werneri 601, 602, 603
Eurygyrus 308
Eurypauropodidae 91
Eurypauropodinae 91
Eurypauropus 91
Eutrichodesmus arcicollaris 87

F

Fagepauropus hesperius 91
Fijiodesmus 74
Fioria tuberculata 276
Formosocephalus longichilatus 88
Fuhrmannodesmidae 67, 71, 168, 171, 172, 524
Fuhrmannodesmini 71
Fusiulus 36, 39
Fusiulus acutus 36
Fusiulus attemsii 36
Fusiulus bilobus 37
Fusiulus capillatus 37
Fusiulus ciliatus 38
Fusiulus cornutus 37
Fusiulus hirosaminus 37
Fusiulus insularumi 39
Fusiulus kiusiensis 37
Fusiulus komatsui 37
Fusiulus koreanus 37
Fusiulus koreanus boninensis 37
Fusiulus koreanus koreanus 37
Fusiulus koreanus tuberculatus 37
Fusiulus kuritai 37
Fusiulus longus 37, 38
Fusiulus onychophora 38
Fusiulus pinetorum 38
Fusiulus pinetorum nivalis 38, 39
Fusiulus quadratus 38
Fusiulus simodanus 38
Fusiulus simplex 38
Fusiulus takakuwai 38
Fusiulus takakuwai coloratus 38
Fusiulus tonggosanensis 38
Fusiulus trapezoidus 39
Fusiulus trigonalis 39
Fusiulus trilobus khuuae 39
Fusiulus trilobus quemoyensis 36
Fusiulus yamashinai 39
Fusiulus yoshidanus 39

G

Galliobates gracilis 278, 326
Galliobatidae 326
Galliocookia balazuci 271, 277
Galliocookia fagei 277
Galliocookia leclerci 271, 277
Geoglomeris duboscqui 275
Geoglomeris granulosa, 275
Geoglomeris provincialis, 275
Geoglomeris subterranea, 275
Geophilella pyrenaica 91
Geophilellidae 91
Geophilidae 32, 88
Geophilinae 88
Geophilus 180, 639
Geophilus balcanicus 236 238
Geophilus carpophagus 180, 206, 207, 601, 639
Geophilus electricus 213, 215, 222, 223, 238
Geophilus flavus 238, 638, 639, 641, 645, 659
Geophilus infossulatus 88
Geophilus insculptus 601, 638, 643, 645
Geophilus linearis 238, 601, 602, 659
Geophilus oligopus 638, 642, 643, 644
Geophilus promontorii 638
Geophilus proximus 222, 223, 238
Geophilus pygmaeus 639
Geophilus rhodopensis 238
Geophilus strictus 238
Glenniea 169
Glenniea bhotiaensis 169
Glenniea indica 169
Glenniea martensi 169
Glenniea minuscula 169
Glenniea perarmata 169
Glomeridae 32, 84, 166, 173
Glomeridea 275, 276, 537
Glomeridella kervillei 275
Glomeris 431, 473, 557, 559, 560, 578, 596
Glomeris annulata 275

Source : MNHN, Paris

Glomeris balcanica 249, 473, 474, 475, 631
Glomeris bicolor 84
Glomeris connexa 211, 212, 275, 431, 432, 433, 434, 578
Glomeris conspersa 180, 258, 275, 647, 649, 652, 655
Glomeris guttata 275
Glomeris helvetica 275
Glomeris hexasticha 199, 249, 473, 474, 475, 488, 559
Glomeris hexasticha intermedia 190, 191, 193, 195, 196, 199, 201, 258, 260
Glomeris humbertiana 275
Glomeris intermedia 275
Glomeris marginata 190, 193, 195, 196, 199, 201, 245, 246, 247, 248, 249, 252, 255, 258, 260, 275, 285, 371, 395, 396, 397, 398, 473, 474, 475, 488, 517, 533, 537, 543, 544, 547, 550, 555, 558, 559, 577, 578, 579, 580, 581, 582, 583, 627, 628, 629, 647, 649, 652, 653, 655
Glomeris pustulata 275
Glomeris transalpina 275
Glomeris undulata 275
Glyphiulus adeloglyphus 85
Glyphiulus anophthalmus 85
Glyphiulus balaszi 85
Glyphiulus formosa 85
Glyphiulus granulatus 85
Glyphiulus multicarinus 85
Glyphiulus pulcher 85
Glyphiulus quadrohamatus 85
Glyphiulus recticullus 85
Glyphiulus tuberculatus 85
Glyphiulus vulgatus 85
Gonebelus sinensis 85
Gonographis adisi 480, 524
Gonoplectus 168, 173
Gonoplectus alius 168
Gonoplectus astutus 85
Gonoplectus bhutanensis 168
Gonoplectus broelemanni 168
Gonoplectus corniger 168
Gonoplectus gracilis 168
Gonoplectus hyatti 168
Gonoplectus lindbergi 168
Gonoplectus malayus 168
Gonoplectus probus 168
Gonoplectus remyi 168
Gonoplectus sulcatus 168
Grammorhabdus 76
Grammorhabdus asperrimum 75
Gyrodrepanum 75
Gyrodrepanum contortipes 75

H

Haasea 154
Haasea flavescens 155, 159, 276
Haasea fonticulorum 451, 452, 454, 457, 458, 459
Haasea norica 152, 156
Habrodesmus duboscqui 585
Hanseniella arborea 528, 607, 609, 612, 613, 614
Haplodesmidae 87, 102, 110, 111
Haplogona oculodistincta 152, 157
Haplogonosoma implicatum 102, 105
Haplophilus subterraneus 221, 222, 223, 224
Haplopodoiulus 321
Haplopodoiulus spathifer 190, 193, 196, 199, 201, 278, 326
Haploporatia eremita 159, 328
Harpagomorpha 75
Harpagomorpha dentata 75
Harpagophoridae 85, 168, 171, 332, 333, 337, 621
Harpaphini 88
Harpolithobius 639
Harpolithobius anodus 238, 601, 639, 640
Harpolithobius anodus dentatus 357
Harpolithobius aseni 238
Harpolithobius banaticus 239, 357
Harpolithobius folkmanovae 237, 239
Harpolithobius gottscheensis 638
Harpolithobius halophilus 226
Harpolithobius hemusi 239
Harpolithobius intermedius 357
Harpolithobius oltenicus 357
Harpolithobius radui 239, 357
Harpolithobius triacanthos 357
Harpolithobius tridentatus 357
Hedinobius hummeli 91
Hedinomorpha biramipedicula 86
Hedinomorpha hummeli 86
Hedinomorpha hummeli svenhedini 86
Helicorthomorpha holstii 86
Helicorthomorpha kosingai 86
Helicorthomorpha ocellata 86
Helicorthomorpha orthogona 86
Helicorthomorpha uncinata 86
Helvetiosoma arvernum 276
Henia angelovi 236, 237, 238
Henia athenarum 601, 603
Henia bicarinata 238, 600, 601
Henia devia 601
Henia hirsuta 600, 601
Henia illyrica 238, 601
Henia vesuviana 659
Henicopidae 91, 226, 303, 304, 305, 341, 346
Henicops 300
Hessebius 226, 232
Hessebius barbipes 225
Hessebius multicalcaratus 266, 267, 268
Heteroiulus 318
Heteroiulus intermedius 318, 326
Heteroporatia bosniensis 211, 212
Heterostoma 442
Hexamerocerata 285, 286
Himalodesmus 169, 173
Himalodesmus audax 169
Himalodesmus benefactor 169
Himalodesmus faustus 169
Himalodesmus parvus 169
Himalodesmus prosperus 169
Himalodesmus pulcher 169
Himalodesmus pygmaeus 169

Source : MNHN, Paris

Himalodesmus vigens 169
Himalomorpha montigena 76
Himantariidae 88
Himantarium gabrielis 238, 600, 601, 603, 659
Himantogonus rufocinctus 75
Hindomorpha granulifera 76
Hingstonia 168, 169, 171, 172, 173
Hingstonia beatae 168
Hingstonia dorjulana 168
Hingstonia eremita 168
Hingstonia falcata 168
Hingstonia fittkaui 168
Hingstonia gogonana 168
Hingstonia pahakholana 168
Hingstonia pelelana 168
Hingstonia perarmata 168
Hingstonia serrata 169
Hingstonia sympatrica 169
Hingstonia variata 169
Hirtodrepanum 169
Hirtodrepanum latigonopum 169
Hirudisoma latum 276
Hirudisoma pyrenaeum 190, 193, 199, 276
Hispaniosoma racovitzai 271, 276
Hyleoglomeris 166, 172, 173
Hyleoglomeris crassipes 166
Hyleoglomeris electa 166
Hyleoglomeris emarginata 84
Hyleoglomeris gorkhalis 167
Hyleoglomeris khumbua 167
Hyleoglomeris modesta 167
Hyleoglomeris nagarjunga 167
Hyleoglomeris sinensis 84
Hyleoglomeris tinjurana 167
Hyleoglomeris venustula 167
Hylomini 87
Hypnosoma exornatum 276
Hypnosoma juberthieorum 276
Hypnosoma pallidum 276
Hypsoiulus alpivagus 278, 326

I

Iberoiulus sarensis 278
Indosphaera 166
Indosphaera curiosa 166
Iulidesmus 74
Iulogona tirolensis cisalpinum 276
Iulus 26, 27
Iulus Americanus 25, 31
Iulus tonginus 39
Iulus peii 84
Iulus vallicola 39

J

Janetschekella valesiaca 276
Japanoiulus lobatus 326
Jonespeltis splendidus 74, 561, 562, 563, 564, 619
Julidae 32, 35, 36, 85, 167, 173, 313, 314, 323, 325, 326, 328, 373, 649
Julidea 272, 278, 537
Julini 315, 321, 326
Juloidea 323
Julus 32, 314, 321, 324
Julus colchicus 326
Julus ghiljarovi 326
Julus jedryczkowskii 326
Julus scandinavius 245, 246, 248, 252, 258, 260, 261, 263, 278, 326, 488, 517
Julus scanicus 321
Julus subalpinus 326
Julus terrestris 211, 212
Junceustreptus brevispinus 85
Junceustreptus browningi 85
Junceustreptus prominulus 85

K

Karpatophyllon 61, 63, 64, 65
Karpatophyllon banaticum 61, 64
Karpatophyllon carpaticum 61, 64
Karpatophyllon dacicum 61, 63, 64
Karpatophyllon polinskii 61, 63, 64
Karteroiulus alaskanus 326
Karteroiulus niger 85
Kaschmiriosoma 170
Kaschmiriosoma contortipes 75, 76, 170
Kaschmiriosoma nulla 170
Kaschmiriosoma pleuroptera 170
Kashmireuma 167, 172
Kashmireuma nepalensis 167
Kashmireuma nielseni 167
Kashmireuma schawalleri 167
Kashmireumatidae 167, 172
Kiulinga jeekeli 88
Kiulinga lobosa 88
Kiusiunum 111
Kiusiunum nodulosum 102, 108
Kiusiunum sekii 102
Kochliopus trivittatus 86
Kophosphaera 166
Kophosphaera brevilamina 166
Kophosphaera devolvens 166
Kophosphaera excavata 166
Kophosphaera excavata mammifera 166
Kophosphaera politissima 166
Kronopeltis occidentalis 76
Kronopolites 170
Kronopolites acuminatus biagrilectus 86
Kronopolites formosanus 86
Kronopolites occidentalis 170
Kronopolites ralphi 86
Kronopolites spiniger 75
Kronopolites svenhedini 86
Kronopolites swinhoei 86
Kronopolites unicolor 75
Kryphioiulus occultus 211, 326, 504, 505

Source : MNHN, Paris

Kylindogaster 111
Kylindogaster nodulosa 102, 109

L

Lamyctes 225, 226, 232
Lamyctes coeculus 226, 227, 232
Lamyctes fulvicornis 215, 219, 227, 240, 266
Lamyctes gracilipes 91
Laterogonopus simplex 76
Leptoiulini 315
Leptoiulus 247, 254, 314
Leptoiulus alemannicus 326
Leptoiulus arelatus 278
Leptoiulus belgicus 245, 247, 248, 258, 278, 326, 647, 649, 651, 652
Leptoiulus bertkaui 258, 278
Leptoiulus brevivelatus 278
Leptoiulus broelemanni 326
Leptoiulus bruyanti 278
Leptoiulus cibdellus 326
Leptoiulus demangei 278
Leptoiulus disparatus 321, 326
Leptoiulus garumnicus 278
Leptoiulus juvenilis 278
Leptoiulus kervillei 245, 247, 248, 252, 278, 488
Leptoiulus legeri 278
Leptoiulus macedonicus 326
Leptoiulus marcomannius 159
Leptoiulus meridionalis 278
Leptoiulus montivagus 278
Leptoiulus odieri 278
Leptoiulus piceus 278
Leptoiulus proximus 211, 212, 249, 326, 431, 432, 433, 434, 478, 479
Leptoiulus remyi 278
Leptoiulus saltuvagus 451, 452, 453, 454, 456, 459
Leptoiulus simplex 488
Leptoiulus simplex glacialis 258, 260, 278
Leptoiulus tanymorphus 326
Leptoiulus umbratilis 190, 193, 195, 201, 203, 278
Leptoiulus uncinatus 278
Leucogeorgiini 173, 318, 326
Levizonus takakuwai 102, 106
Listrocheiritium 154, 156, 158
Listrocheiritium cervinum 152, 156
Listrocheiritium nibelungiacum 156
Listrocheiritium noricum 152, 156
Listrocheiritium septentrionale 152, 156, 158
Lithobiidae 32, 90, 227, 295, 303, 304, 341, 346, 660
Lithobiinae 90
Lithobius 27, 28, 180, 226, 232, 240, 267, 351, 353, 354, 360 366, 386, 393, 381, 416, 418, 422, 423, 424, 429, 639
Lithobius acuminatus 658, 659
Lithobius aeruginosus 239
Lithobius aeruginosus mongolicus 90
Lithobius agilis 239, 601, 639, 640
Lithobius agilis pannonicus 357
Lithobius allotyphlus 357
Lithobius ankarensis praecursor 227
Lithobius anornatus 90
Lithobius asperatus 91
Lithobius audax 239
Lithobius aulacopus 357
Lithobius balcanicus 239
Lithobius beroni 237, 239
Lithobius beschkovi 239, 601, 604
Lithobius bidivisa 90
Lithobius bifidus 239
Lithobius bogdoulensis 90
Lithobius borealis 190, 191, 266, 357
Lithobius borisi 236
Lithobius brignolii 601, 602
Lithobius bulgaricus 239, 357
Lithobius burzenlandicus 239
Lithobius calcaratus 190, 352, 357, 658, 659
Lithobius carinatus 225, 232, 601
Lithobius castaneus 180, 190, 357, 638, 642, 658, 659
Lithobius catascaphius 239
Lithobius cavernicola 357
Lithobius christovici 239
Lithobius coeculus 226, 227, 232
Lithobius crassipes 180, 215, 219, 222, 223, 239, 352, 366, 601, 602
Lithobius cronebergii 266, 267, 268
Lithobius crypticola 357
Lithobius curtipes 222, 223, 239, 352
Lithobius cyrtopus 266, 267, 357
Lithobius dalmaticus 239
Lithobius decapolitus 357
Lithobius decessus 90
Lithobius dentatus 638, 639, 644, 645
Lithobius diampolisi 239
Lithobius dobrogicus 239
Lithobius duboscqui 190, 239, 266
Lithobius electron 236, 239
Lithobius erratus 90
Lithobius erythrocephalus 222, 223, 226, 232, 236, 239, 266, 267, 352, 357, 601, 602
Lithobius erythrocephalus borisi 604
Lithobius fagniezi 357
Lithobius fasciatus 225
Lithobius forficatus 22, 180, 190, 213, 215, 216, 221, 222, 223, 239, 266, 267, 268, 305, 352, 355, 357, 366, 369, 385, 391, 392, 393, 403, 404, 405, 407, 411, 415, 421, 422, 424, 638, 642, 643, 644, 645, 657, 658, 659, 660, 661
Lithobius gantoensis 90
Lithobius glaciei 236, 239
Lithobius golemanskyi 237, 239
Lithobius hauseri 600, 601
Lithobius hummeli 90
Lithobius inermis 206, 207, 208, 357
Lithobius irregularis 90
Lithobius jangsteanus 90
Lithobius jurinici 236, 239
Lithobius kansuanus 90
Lithobius kiayiensis 90
Lithobius lakatnicensis 239, 601, 604

Source : MNHN, Paris

Lithobius lapidicola 239, 266, 357, 601, 602, 638, 639, 641, 642, 644, 657 658, 659
Lithobius latro 239, 357, 601, 638, 639, 642, 643
Lithobius litoralis 227
Lithobius lucifugus 239, 266, 267, 357, 601, 602
Lithobius lusitanus 206, 207, 208, 644, 645
Lithobius lusitanus tataricus 266, 267, 268
Lithobius luteus 357
Lithobius macilentus 638, 639, 640, 641, 642, 643, 644, 645
Lithobius macrops 225
Lithobius maculipes 236, 239
Lithobius matici matici 357
Lithobius melanops 215, 219, 222, 223, 266, 267, 352, 357, 640, 642
Lithobius microps 190, 213, 215, 216, 219, 221, 222, 239, 266, 267, 268, 352 357, 601, 602
Lithobius mongolellus 90
Lithobius mongolicus 90
Lithobius mongolomedius 90
Lithobius mutabilis 215, 219, 239, 240, 266, 357, 601, 602
Lithobius muticus 239, 357, 601
Lithobius nicoeensis 357
Lithobius nigrifrons 239, 357
Lithobius nigripalpis 239, 601, 602
Lithobius nodulipes 357, 638, 639, 641, 645
Lithobius oglednicus 239
Lithobius ongi 90
Lithobius parietum 239, 266, 267, 357
Lithobius parvicornis 225, 232
Lithobius pelidnus 239, 266, 267, 357
Lithobius peregrinus 237, 239, 357, 601, 602
Lithobius piceus 190, 239, 266, 267, 357
Lithobius piceus gracilitarsis 360, 361
Lithobius pilicornis 190, 206, 207, 208, 357, 359, 360
Lithobius popovi 239
Lithobius praecursor 227
Lithobius proximus 239, 266, 267, 268
Lithobius punctulatus vasconicus 357
Lithobius pusillus 239
Lithobius pustulatus 239
Lithobius pygmaeus 640, 642
Lithobius ribauti 357
Lithobius romanus 659
Lithobius rufus 90
Lithobius rugosus 91
Lithobius ruschovensis 239
Lithobius rylaicus 236, 239
Lithobius schuleri 601, 602
Lithobius silvivagus 357
Lithobius speluncarum 357
Lithobius strandzanicus 237, 239
Lithobius sulcifemoralis 90
Lithobius tenebrosus 266, 267, 352, 601, 603, 643
Lithobius tethidis 90
Lithobius tetrophthalmus 90
Lithobius thracicus 236, 239
Lithobius tiasnatensis 236, 239
Lithobius totevi 240
Lithobius trebinjanus 240
Lithobius trichopus 90
Lithobius tricuspis 190, 240, 357, 641
Lithobius troglodytes scutigeropsis 357
Lithobius tylopus 658, 659
Lithobius typhlus 357
Lithobius uniunguis 240
Lithobius validus 266, 645
Lithobius variegatus 357
Lithobius variegatus rubriceps 190, 191, 206, 207, 208
Lithobius viriatus 226, 232, 240, 266, 267, 601, 602
Lithobius vizicae 240
Lithobius vosseleri 225
Lithobius zelazovae 240
Lithobius (Dacolithobius) domogledicus 357
Lithobius (Monotarsobius) aeruginosus 357
Lithobius (Monotarsobius) baloghi 357
Lithobius (Monotarsobius) biunguiculatus 357
Lithobius (Monotarsobius) burzenlandicus 357
Lithobius (Monotarsobius) crassipes 357
Lithobius (Monotarsobius) curtipes 357
Lithobius (Monotarsobius) dobrogicus 357
Lithobius (Monotarsobius) duboscqui 357
Lithobius (Monotarsobius) dudichi 357
Lithobius (Monotarsobius) microps 357
Lithobius (Monotarsobius) pustulatus 357
Lithobius (Monotarsobius) sciticus 357
Lithobius (Monotarsobius) subterraneus 357
Lithobius (Polybothrus) fasciatus graecus var. *fasciatograecus* 227
Lithobius (Thracolithobius) dacicus 357
Lithobius (Thracolithobius) inexpectatus 357
Loboglomeris haasi 190, 193
Loboglomeris pyrenaica 275
Loboglomeris rugifera 275
Lophoproctidae 84, 123
Lophoproctinus inferus 275
Lophoproctinus inferus maurus 123, 124, 125
Lophoproctus 133
Lophoproctus jeanneli 275
Lophoproctus lucidus 275
Lophoproctus madecassus 125
Lophoturus 127, 128, 134
Lophoturus aequatus 127, 128, 133, 134
Lophoturus madecassus 113, 123, 124, 127, 133
Lophoturus niveus 133, 134
Lophoturus okinawai 84

M

Macheiriophoron 54, 58
Macheiriophoron aelleni 53, 54, 55, 57, 58
Macheiriophoron alemannicum 53, 54, 55, 57, 58
Macheiriophoron alemannicum genuinum 54, 58
Macheiriophoron alemannicum globosum 54, 57, 58
Macheiriophoron alemannicum rotundatum 54, 58
Macheiriophoron alemannicum triarticulatum 54, 58
Macheiriophoron cervinum 53, 54, 55, 57, 58
Macheiriophoron cervinum brevidentatum 54, 55, 58
Macheiriophoron montivagum 58
Macheiriophoron montivagum silvaticum 58

Source : MNHN, Paris

Macheiriophoron serratum 54, 59
Macheiriophoron silvaticum 54, 58
Macheiriophoron silvaticum hessei 54
Macheiriophoron verhoeffi 54, 59
Macheiriophoron verhoeffi excavatum 55, 59
Macheiriophoron verhoeffi genuinum 59
Macheiriophoron wehranum 54, 59
Macheiriophoron wehranum brevidentatum 55
Macheiriophoron wehranum calcivagum 55, 59
Macheiriophoron wehranum clavigerum 55, 59
Macheiriophoron wehranum genuinum 59
Macheiriophoron wehranum quadridentatum 59
Macheiroiulus compressicauda 326
Macheiroiulus libicus 319, 320, 326
Macrosternodesmidae 101
Macrosternodesmus 101
Macrosternodesmus palicola 245, 246, 247, 248, 258, 277, 488
Macroxenodes 121, 127, 128, 133
Macroxenodes bartschi 121, 133
Macroxenus 120, 121
Macroxenus caingangensis 121, 125
Macroxenus enghoffi 113, 117, 118, 121, 123, 125
Macroxenus rubromarginatus 121, 125
Magidesmus 169
Magidesmus affinis 169
Magidesmus bhutanensis 169
Mandarinopus gracilipes 87
Marquetiella auriculata 276
Marquetiella lunata 276
Marquetiella lunatum 190, 193, 196, 199, 201
Marquetiella pyrenaica 276
Martensodesmus 169
Martensodesmus bicuspidatus 169
Martensodesmus excornis 169
Martensodesmus himalayensis 169
Martensodesmus nagarjungicus 169
Martensodesmus sherpa 169
Martensosoma 170
Martensosoma elegans 170
Martensosoma foveatum 170
Martensosoma schawalleri 170
Martensosoma silvestre 170
Martensosoma splendens 170
Martensosoma unicolor 170
Mastigona bosniense 328
Mastigonodesmus destefani 277
Mastigonodesmus fagniezi 271, 277
Mastigonodesmus lopezi 271, 277
Mastigophorophyllidae 62, 328
Mastigophorophyllon 61, 62, 63, 64, 65
Mastigophorophyllon aberratum 61, 62, 64
Mastigophorophyllon alpivagum 61, 62, 64
Mastigophorophyllon banarescui 61, 62
Mastigophorophyllon banaticum 64
Mastigophorophyllon bohemicum 61, 62, 64
Mastigophorophyllon bulgaricum 61, 62, 64
Mastigophorophyllon bulgaricum pirinicum 61, 62, 64
Mastigophorophyllon carpaticum 61, 62, 63, 64
Mastigophorophyllon cirriferum 61, 62, 64
Mastigophorophyllon crinitum 61, 62, 64
Mastigophorophyllon crinitum huculicum 61, 62, 64
Mastigophorophyllon deubeli 61, 62, 64
Mastigophorophyllon giliarovi 63
Mastigophorophyllon jickelii 61, 62, 64
Mastigophorophyllon penicilligerum 61, 62, 64
Mastigophorophyllon saxonicum 61, 62, 63, 64
Mastigophorophyllon serrulatum 61, 62, 63, 64
Mastigophorophyllon serrulatum apiculatum 61, 62, 64
Mastigophorophyllon transsilvanicum 61, 62, 64
Mecistocephalidae 78
Mecistocephalinae 88
Mecistocephalus brevisternalis 89
Mecistocephalus diversisternus 89
Mecistocephalus fenestratus 89
Mecistocephalus indecorus 89
Mecistocephalus insularis 89
Mecistocephalus insulomontanus 89
Mecistocephalus japonicus 89
Mecistocephalus mikado 88
Mecistocephalus mirandus 89
Mecistocephalus monticolens 89
Mecistocephalus multidentatus 89
Mecistocephalus nannocornis 89
Mecistocephalus ongi 89
Mecistocephalus punctifrons 89
Mecistocephalus rubriceps 88
Mecistocephalus smithi 89
Mecistocephalus takakuwai 89
Megalotylidae 167, 172
Megaphyllum 314, 317, 318, 325
Megaphyllum adanense 317, 326
Megaphyllum bosniense 326
Megaphyllum brachyurum 318, 326
Megaphyllum geniculatum 318, 326
Megaphyllum hercules 317, 326
Megaphyllum projectum kochi 431, 432, 433, 434
Megaphyllum rossicum 326
Megaphyllum taygeti 326
Megaphyllum tenenbaumi 326
Megaphyllum unilineatum 40
Melogona gallica 245, 248, 258, 259, 260, 262, 277, 488, 509, 512, 513, 533, 537, 541, 550
Melogona scutellare 245, 248, 277, 509, 513
Melogona voigti 509, 510, 511, 512, 513, 514
Mesoblaniulus serrula 278
Mesoiulus ciliciensis 315, 326
Mesomeritius indivisus 326
Mestosoma hylaeicum 524
Metaiulini 320, 324, 326
Metaiulus pratensis 245, 246, 247, 248, 249, 250, 278, 320, 326
Metamastigophorophyllon 61, 63
Microchordeuma gallicum 509, 512, 513, 541
Millotauropus silvestrii 286
Mimops orientalis 90
Monacobates monoecensis 278
Mongoliulidae 85, 326
Monographis 166
Monographis mirus 166
Monographis tamoyoensis 122
Monotarsobius 225, 226, 231, 232, 639

Source : MNHN, Paris

Monotarsobius aeruginosus 266, 267, 638, 639, 640, 641, 642, 643, 644
Monotarsobius alticus 90
Monotarsobius argaeensis 90
Monotarsobius barbipes 225
Monotarsobius bolognai 226, 231, 232
Monotarsobius crassipes 90, 226, 231, 232, 266, 267
Monotarsobius crassipes holstii 90
Monotarsobius crassus 90
Monotarsobius curtipes 266, 267, 268
Monotarsobius kaszabi 90
Monotarsobius microps 266
Monotarsobius obtusus 90
Monotarsobius ramulosus 90
Monotarsobius rhysus 90
Monotarsobius schizus 231
Monotarsobius sseliwanoffi 266, 267, 268
Monotarsobius teldanensis 225, 229, 231, 232
Moojenodesmus pumilus 524
Moojenodesmus susannae 524
Muyudesmus obliteratus 524
Mycogona germanica 277, 329
Mycogona germanicum 258, 647, 649, 650, 652, 653, 655

N

Nannophilus ariadnae 600, 601
Nanogona balazuci 276
Nanogona cebennica 276
Nanogona davidi 276
Nanogona digitata 276
Nanogona polydesmoides 245, 246, 248, 249, 276
Nanogona uncinata 276
Narceus annularis 515
Necrophloeophagus flavus 213, 215, 221, 222, 223
Nedyopodini 87
Nedyopus patrioticus 87
Nedyopus tambanus 102, 105
Nemasoma varicorne 210, 211, 212, 245, 246, 248, 250, 258, 278, 326, 328, 488, 521
Nemasomatidae 85, 326, 328
Nepalella 167, 172, 173
Nepalella deharvengi 167, 168
Nepalella gairiensis 167
Nepalella gunsa 167
Nepalella jaljalae 167
Nepalella khumbua 167
Nepalella phulcokia 167
Nepalella ringmoensis 167
Nepalella taplejunga 167
Nepalella thodunga 167
Nepalella tragsindola 167
Nepalmatoiulus 35, 168, 172, 173, 318, 326
Nepalmatoiulus appendiculatus 168
Nepalmatoiulus birmanicus 318, 326
Nepalmatoiulus brachymeritus 86
Nepalmatoiulus deharvengi 168
Nepalmatoiulus dhaulagiri 168
Nepalmatoiulus eulobos 86
Nepalmatoiulus fraterdraconis 86
Nepalmatoiulus generalis 168
Nepalmatoiulus hyalilobus 168
Nepalmatoiulus ivanloebli 168, 172
Nepalmatoiulus juxtapositus 168
Nepalmatoiulus martensi 168
Nepalmatoiulus mauriesi 168
Nepalmatoiulus nigrescens 168
Nepalmatoiulus pineti 168
Nepalmatoiulus polyakis 86
Nepalmatoiulus rhaphimeritus 85
Nepalmatoiulus rugiflagrum 168
Nepalmatoiulus smetanai 168
Nepalmatoiulus sympatricus 168
Nepalmatoiulus tibetanus 85
Nepalmatoiulus uncus 168
Nepalmatoiulus wuermlii 168
Nepalmatoiulus yunnanensis 86
Nepalmatoiulus zachonoides 168
Nepalomorpha 170
Nepalomorpha arunensis 170
Nepalomorpha hirsuta 170
Nepalomorpha kuznetsovi 170
Nepalomorpha spinigera 170
Nesoporogaster hispanica 190
Newportia 294, 295
Niponia 111
Niponia nodulosa 87, 102, 108
Niponia simplexus 88
Nodocephalus dooi 89
Nodocephalus edentulus 89
Nodocephalus pauroporus 89
Nopoiulus kochii 244, 245, 247, 248, 278
Nopoiulus minutus 244
Nopoiulus venustus 211, 244

O

Occitaniulus rouchi 278
Occitanocookia hirsuta 271, 277
Ochogona caroli 451, 452, 453, 454, 457, 459
Ochogona gallitarum 276
Odontopygidae 332, 333, 337, 572, 574, 621
Okeanobates serratus 326
Okeanobatidae 326
Ommatoiulus 314, 322, 324, 325, 373, 374, 592
Ommatoiulus albolineatus 278
Ommatoiulus apunctulatus 588
Ommatoiulus cingulatus 326
Ommatoiulus corsicus 278
Ommatoiulus gauthieri 180, 182
Ommatoiulus haackeri 278
Ommatoiulus illicis 278
Ommatoiulus imminutus 278
Ommatoiulus kessleri 322, 326
Ommatoiulus lapidarius 326
Ommatoiulus lienhardti 278
Ommatoiulus moreleti 322, 326, 375, 470, 517, 588
Ommatoiulus navasi 322, 326
Ommatoiulus nivalis 326

Source : MNHN, Paris

Ommatoiulus osellai 326
Ommatoiulus oxypygus 326
Ommatoiulus robustus 190, 193, 199, 201, 203
Ommatoiulus rutilans 258, 259, 260, 262, 278, 322, 326, 628
Ommatoiulus sabulosus 190, 193, 201, 245, 246, 248, 250, 254, 258, 259, 260, 261, 278, 326, 373, 374, 375, 376, 377, 380, 381, 382, 431, 432, 433, 434, 537, 550, 587, 588, 589, 590, 592, 593, 595, 596, 597, 628, 647, 649, 651, 652, 654
Ommatoiulus sabulosus aimatopodus 588
Ommatoiulus sabulosus punctatus 576
Onciurosoma adisi 524
Oncoiulini 318, 319, 326
Oncoiulus 314
Onychoglomeris castanea 275
Onychophora 39,139, 141, 142, 143, 148, 149, 483, 493, 494
Ooperipatellus 141, 142, 143, 144, 145, 146, 147, 148
Ooperipatellus insignis 139, 141, 142, 147, 148
Ooperipatellus nanus 143
Ooperipatellus viridimaculatus 147, 148
Ooperipatus 140, 143
Ooperipatus decoratus 140, 144, 145, 146, 147, 148
Ooperipatus insignis 140
Ooperipatus oviparus 140, 145, 146
Ophiodesmus albonanus 211, 245, 246, 247, 248, 277
Ophyiulus 321
Ophyiulus bastiensis 278
Ophyiulus chilopogon 278, 326
Ophyiulus corsicus 278
Ophyiulus fallax 210, 211, 212
Ophyiulus germanicus 326
Ophyiulus major 321, 326
Ophyiulus napolitanus 278
Ophyiulus pilosus 245, 246, 248, 249, 252, 278, 326, 398, 478, 479, 564
Ophyiulus renosensis 278
Ophyiulus targionii 326
Opisotretidae 102, 110, 111, 169, 171
Opisthocheiron canayerensis 271, 274, 276
Opisthocheiron cornutum 276
Opisthocheiron elegans 276, 627, 628, 629, 630
Opisthocheiron fallax 276
Opisthocheiron lacazei 276
Opisthocheiron penicillatum 276
Origmatogona kimeorum 271, 276
Orinisobates gracilis 85
Orinisobates 326
Orophini 88
Orophosoma 170, 171, 172
Orophosoma fechteri 170
Orophosoma hingstoni 86, 170
Orophosoma simulans 86, 170
Orphnaeus brevilabiatus 88
Orthochordeumella fulva 159, 277
Orthochordeumella leclerci 271, 277
Orthochordeumella pallida 258, 259, 260, 262, 277, 488
Orthochordeumella pyrenaica 277
Orthomorpha 75, 170
Orthomorpha affinis 87
Orthomorpha almorensis 75, 170
Orthomorpha bisulcata 87
Orthomorpha circularis 87
Orthomorpha coarctata 86, 102, 105, 170
Orthomorpha coonoorensis 75
Orthomorpha corticina 87
Orthomorpha dentata 75
Orthomorpha endeusa 87
Orthomorpha flavomarginata 87
Orthomorpha nordenskjoeldi 87
Orthomorpha penicillata 87
Orthomorpha (Kalorthomorpha) almorensis 74
Orthomorpha (Kalorthomorpha) coonoorensis 74
Orthomorpha (Kalorthomorpha) dentata 74
Orthomorpha (Kalorthomorpha) ursula 74
Orthoporoides 333, 334
Orthoporoides pyrocephalus 334, 336, 337
Orthoporus 623
Orthoporus ornatus 397, 470, 471
Orthoporus pyrocephalus 333
Oryidae 88, 301
Otocryptops 295, 442
Otocryptops rubiginosa 90
Otocryptops sexspinosus 90
Otostigminae 89, 442, 447
Otostigmus 294, 295
Otostigmus aculeatus 89
Otostigmus astenus 89
Otostigmus frigidus 89
Otostigmus insularis 89
Otostigmus malayanus 89
Otostigmus multispinosus 89
Otostigmus politus 89
Otostigmus politus mandschurius 89
Otostigmus politus pigmentatus 89
Otostigmus scaber 89
Otostigmus striatus 89
Oxidus 170
Oxidus corcifera 87
Oxidus gracilis 86, 102, 105, 170, 211, 247, 255, 258, 277, 431, 432, 433, 434
Oxydesmidae 101

P

Pachydesmus attemsi 88
Pachyiulini 313, 315, 324, 326
Pachyiulus 313, 314, 315, 596
Pachyiulus flavipes 326
Pachyiulus fuscipes 588, 589, 592
Pachyiulus varius 278
Pachymerinae 88
Pachymerium atticum 88
Pachymerium ferrugineum 88, 206, 207, 222, 223, 238, 601, 602, 659
Pachymerium ferrugineum insulanum 236
Pachymerium flavum 238
Pachypodoiulus eurypus 326
Pacidesmus sinensis 87
Pacifiiulus imbricatus 326

Source : MNHN, Paris

Paectophyllini 313, 315, 319, 320, 324, 326
Paectophyllum escherichii 320, 326
Paeromopodidae 326
Paeromopodoidea 326
Pamelaphe lacustris 88
Parabilingulus aramulus 85
Parachordeuma broelemanni 277
Paracortina (Altum) carinata 86
Paracortina (Altum) serrata 86
Paracortina (Altum) viriosa 86
Paracortina (Relictus) stimula 86
Paracortina (Relictus) thallina 86
Paracortina 309
Paracortina leptoclada 86, 307, 308, 309, 310
Paracortina voluta 86, 307, 308, 309, 310
Paracortinidae 86, 307, 308
Paracryptops 294, 295
Paradoxosoma 73
Paradoxosomatidae 73, 74, 86, 87, 102, 104, 105, 110, 169, 171, 173, 524
Paradoxosomatidea 86, 277
Paradoxosomatinae 74, 86
Paradoxosomatini 173
Paradoxosomatoidea 86
Parafontaria ishiii 102
Parafontaria laminata armigera 102, 103, 106
Paraiulidae 85, 326
Paramastigophorophyllon 62
Paranedyopus 170, 173
Paranedyopus affinis 170
Paranedyopus cylindricus 76, 170
Paranedyopus elongissimus 76, 170
Paranedyopus martensi 170
Paranedyopus rufocinctus 75
Paranedyopus schawalleri 170
Paranedyopus similis 170
Paranedyopus simplex 75
Paranedyopus subcylindricus 75
Paranedyopus ursula 75
Parapachyiulus recessus 326
Parapauroplus monodentus 87
Paraplanes svenhedini 88
Parchondromorpha 75
Parchondromorpha coonoorensis 75
Parchondromorpha indica 76
Parchondromorpha similis 76
Parfusiulus 39
Parorthomorpha 170
Parorthomorpha affinis 170
Parorthomorpha granulosa 170
Parorthomorpha intermedia 170
Parorthomorpha longiseta 170
Parorthomorpha nyakensis 170
Parorthomorpha philosophica 170
Parorthomorpha spectabilis 170
Parorthomorpha tergalis 170
Parorthomorpha tuberculata 170
Pauropodidae 91
Pauropsxenus vilhenae 122
Pauropus bifurcus 91
Pauropus longiramus 91
Pectiniunguis 79
Peltopodoiulus schestoperovi 326
Penicillata 84, 113, 127
Perapolydesmus progressus 277
Pericambalidae 85
Peripatidae 493, 494
Peripatoides leuckarti 140
Peripatopsidae 139, 140, 141, 142
Peripatus 140
Peripatus insignis 140, 143
Phalloiulus distinctus 180
Phyletodesmus 74
Physobolidae 168, 171
Physobolus 168
Physobolus olivaceus 168
Platydesmidea 276
Pleurogeophilus mediterraneus 601, 602
Pleurogeophilus takakuwai 88
Pleurolithobius jonicus 237, 240
Pleurolithobius orientis 601
Pleurolithobius patriarchalis 600, 601, 602
Plutonium 294, 295, 296, 297, 301, 441
Plutonium zwierlainii 296
Pocillidorsus dorsiangulatus 87
Podoglyphiulus 168
Podoglyphiulus elegans nepalensis 168
Polybothridae 90
Polybothrus fasciatus 225, 226, 227
Polydesmidae 32, 73, 87, 101, 102, 106, 117, 111, 169, 173, 650
Polydesmidea 87, 277, 537
Polydesmoidea 87
Polydesmus 173, 244, 480, 481
Polydesmus angustus 245, 246, 247, 248, 249, 258, 260, 262, 277, 488,533, 537, 542, 543, 547, 550
Polydesmus asthenestatus 277
Polydesmus barbierii 277
Polydesmus complanatus 211, 212, 249, 250, 431, 432, 433, 434
Polydesmus coriaceus 250, 277
Polydesmus coriaceus coriaceus 190, 193, 196, 199
Polydesmus corsicus 277
Polydesmus denticulatus 245, 246, 248, 250, 254, 258, 260, 262, 277, 477, 478, 479, 480, 481, 488, 489
Polydesmus gallicus 245, 246, 248
Polydesmus germanicus 277
Polydesmus hamatus 87, 277
Polydesmus helveticus 159, 277
Polydesmus incisus 277
Polydesmus inconstans 211, 212, 245, 246, 248, 258, 260, 277, 647, 649, 650, 651, 652, 654
Polydesmus japonicus 102, 107
Polydesmus liber 87
Polydesmus mistrei 277
Polydesmus moorei 88
Polydesmus niveus 277
Polydesmus paludicola 88
Polydesmus plicatus 277
Polydesmus racovitzai 190, 193, 277
Polydesmus raffardi 277
Polydesmus rothi 154, 160

Source : MNHN, Paris

Polydesmus superus 280
Polydesmus taranus 277
Polydesmus testaceus 245, 246, 247, 248, 250, 258, 259, 260, 262, 277
Polydesmus troglobius 277
Polydesmus xanthocrepis 154, 157, 160
Polydrepanini 74, 75, 86
Polydrepanum 75, 76
Polydrepanum horridum 76
Polydrepanum implicatum 75, 76
Polydrepanum tamilum 75
Polylobosoma roseipes 87
Polypauropidae 91
Polyxenes (sic!) 127
Polyxenida 84, 166, 275
Polyxenidae 32, 84, 114, 123, 166
Polyxenidea 275
Polyxenus 117, 127, 128, 132, 133, 166, 285, 287
Polyxenus anacapensis 127, 132, 133
Polyxenus bartschi 127, 128, 133
Polyxenus chalcidicus 114, 116, 117, 125
Polyxenus fasciculatus 113, 114, 123, 124, 125, 127, 128, 129, 130, 131
Polyxenus fasciculatus pallidus 128
Polyxenus fasciculatus victoriensis 128
Polyxenus hangzoensis 84, 133
Polyxenus koreanus 133
Polyxenus lagurus 113, 114, 116, 123, 124, 125, 127, 129, 130, 131, 245, 246, 247, 248, 250, 258, 275, 286, 628, 629, 630
Polyxenus lapidicola 117
Polyxenus macedonicus 117, 275
Polyxenus oromii 113, 114, 116, 117, 123, 125
Polyxenus pœcilus 133
Polyxenus pugetensis 127, 129, 130, 131
Polyxenus shinoharai 133
Polyxenus tuberculatus 127, 128
Polyzonidae 32
Polyzoniidea 276
Polyzonium germanicum 211, 245, 246,248, 250, 252, 254, 276, 461, 462, 463, 465, 466, 469, 470, 471, 627, 628, 629, 631, 632, 633
Prionomatis 102, 107, 111
Prionopeltis planatus 76
Prolamnonyx holstii 89
Prolamnonyx sauteri 89
Prosopodesmus jacobsoni 87
Prostemmiulus adisi 524
Prostemmiulus amazonicus 524
Prostemmiulus wellingtoni 524
Proteroiulus broelemanni 278
Proteroiulus fuscus 211, 212, 245, 246, 248, 250, 252, 254, 258, 278
Protoglomeris vasconica 190, 193, 195, 196, 199, 201, 275
Pselaphognatha 285, 286, 287
Pseudocatapyrgodesmus 111
Pseudodesmus 167
Pseudonannolenidae 524
Pseudonemasoma femorotuberculata 326
Pseudonemasomatidae 326
Pseudosphaeroparia 169
Pseudosphaeroparia cavernicola 169
Pteridoiulini 315, 317, 324, 326
Pteridoiulus 324
Pteridoiulus aspidiorum 317, 326
Pterozonium 167
Pterozonium cingulatum 167
Pterozonium coniceps 167
Pterozonium larwoodi 167
Pterygotergidae 91
Pterygotergum svenhedini 91
Pyreneosoma barbieri 276
Pyreneosoma bessoni 276
Pyreneosoma digitatum 276
Pyreneosoma ribauti 276
Pyrgocyphosoma 154
Pyrgocyphosoma dalmazzense 277
Pyrgocyphosoma doriae 277
Pyrgocyphosoma titianum 152, 154
Pyrgodesmidae 88, 102, 108, 110, 111, 170, 171, 524

R

Relictus 309
Relictus stimulus 307, 308, 309, 310
Relictus thallinus 307, 308, 309, 310
Rhapidostreptus 411, 413, 415, 416, 417, 418, 422, 423, 424, 429
Rhapidostreptus virgator 411, 412, 414, 417, 421, 422, 424, 434
Rhipidopeltis 102, 110, 111
Rhodesiostreptus matabele 572
Rhodopiella beroni 326
Rhopaloiulidae 323, 324, 326
Rhopaloiulus cameratanus 326
Rhymogona 45, 46, 48, 49, 50, 53, 54, 57, 58, 152, 154, 155, 156, 159
Rhymogona aelleni 49, 53, 55, 57
Rhymogona alemannica 46, 48, 49, 50, 53, 54, 55, 57, 152, 271, 277
Rhymogona alemannica alsaticum 54
Rhymogona alemannica globosum 54, 57
Rhymogona alemannica rotundatum 54
Rhymogona alemannica triarticulatum 54 ,57
Rhymogona cervina 46, 47, 48, 49, 50, 53, 54, 55, 58, 152, 159, 271, 277
Rhymogona cervina brevidentatum 54
Rhymogona montivaga 46, 47, 48, 49, 50, 53, 55, 57, 58, 271, 277
Rhymogona montivaga alemannica 56, 58
Rhymogona montivaga cervina 56, 58
Rhymogona montivaga hessei 49, 55, 58
Rhymogona montivaga montivaga 49, 56, 58
Rhymogona montivaga serrata 56, 59
Rhymogona montivaga verhoeffi 56, 59
Rhymogona montivaga wehrana 56, 59
Rhymogona serrata 48, 49, 50, 53, 54, 55, 57, 59, 152
Rhymogona silvatica 53, 55, 58, 271
Rhymogona silvatica hessei 271
Rhymogona verhoeffi 48,49, 50, 53, 54, 55, 57, 59, 152

Source : MNHN, Paris

Rhymogona verhoeffi excavatum 54
Rhymogona wehrana 48, 49, 50, 53, 55, 57, 59, 152
Rhymogona wehrana calcivagum 54
Rhymogona wehrana clavigerum 54
Rhymogona wehrana genuinum 54
Rhymogona wehrana quadridentatum 54
Rhysida 294, 295, 441, 442, 444, 447, 448
Rhysida lithobioides 90
Rhysida longipes 90
Rhysida longipes brevicornis 90
Rhysida mandchurica 89
Rhysida nuda brevicornuta 90
Rhysida nuda immarginata 90
Rhysida nuda nuda 89
Rhysida nuda togoensis 441, 442, 443, 447, 448
Rhysida yanagiharai 90
Rhysodesmus cohaesivus 88
Rhysodesmus contiguus 88
Ribautiella 610
Ribautiella amazonica 607, 609, 610, 614
Riukiaria 102, 106
Riukiaria capaca 88
Riukiaria holstii 88
Riukiaria neptuna 88
Riukiaria ochraceus 88
Riukiaria taiwanalis 88
Riukiaria taiwanus 88
Riukiaria uraensis 88
Riukiaria variata 88
Rossiulus kessleri 515, 516, 517, 518 521

S

Schendyla 180, 639
Schendyla carniolensis 638, 639, 640, 641, 643, 644
Schendyla delicatula 238
Schendyla montana 238, 601, 603
Schendyla nemorensis 206, 207, 208, 213, 215, 221, 222, 223, 238, 638, 643, 644, 645, 659
Schendyla walachica 238
Schendylidae 79, 88
Schendylinae 88
Schendylurus 79
Schizophyllini 322, 324, 326
Schizophyllum 314
Schizophyllum sabulosum 516
Scolioplanes maritimus japonicus 88
Scolioplanes transsilvanicum 88
Scolopendra 26, 27, 29, 31, 32, 82, 180, 236, 294, 295, 423, 424, 441, 447, 495, 497, 498
Scolopendra Americana (sic!) 25, 31
Scolopendra calcarata 89
Scolopendra canidens 448
Scolopendra cingulata 89, 206, 207, 208, 236, 238, 366, 421, 422, 423, 429, 442, 600, 601, 603
Scolopendra cingulata thracia 236
Scolopendra dalmatica 600, 601
Scolopendra electrica 32
Scolopendra marina 27, 32
Scolopendra mazbii 83, 89
Scolopendra mirabilis 448
Scolopendra morsitans 89, 236, 441, 442, 444, 447, 448, 495, 497, 498
Scolopendra multidens 89
Scolopendra mutilans 89
Scolopendra oraniensis 429
Scolopendra phosphorea 32
Scolopendra rapax 89
Scolopendra rugosa 89
Scolopendra septemspinosa 89
Scolopendra subspinipes 89
Scolopendra subspinipes dehaani 89
Scolopendra subspinipes japonica 89
Scolopendra terrestris 27
Scolopendra valida 441, 442, 444, 446, 447, 448
Scolopendrellidae 137, 609, 610, 611, 614
Scolopendrellopsis 137
Scolopendrellopsis (Symphylellopsis) pauli 137
Scolopendrellopsis (Symphylellopsis) selgae 137
Scolopendrellopsis tropicus 614
Scolopendria marina 32
Scolopendria terrestris 32
Scolopendridae 32, 89, 294, 441
Scolopendrinae 89, 442, 447
Scolopocryptops 294, 295
Scolopocryptops brolemanni 90
Scolopocryptops ferrugineus 294
Scolopocryptopsinae 90
Scutigera 240, 300, 301,346, 437
Scutigera coleoptrata 91, 180, 206, 207, 240, 305, 437, 438, 439, 440, 600, 601
Scutigera complanata 91
Scutigera hispida 91
Scutigera longicornis clunifera 91
Scutigera sinensis 91
Scutigera sinuata 91
Scutigerella immaculata 91
Scutigerellidae 91, 612, 614
Scutigeridae 91
Scutogona jeanneli 277
Semenellogon 74
Semiosoma bardei 277
Semiosoma devillei 277
Serboiulus lucifugus 321
Serradium 101
Sholaphilus 169, 171, 172
Sholaphilus asceticus 169
Sholaphilus dalai 169
Sholaphilus gompa 169
Sholaphilus lama 169
Sholaphilus martensi 169
Sholaphilus monachus 169
Sibiriulus dentiger 326
Sichotanus mandschuricus 87
Sigibius 639
Sigipinius grahami 87
Sinocallipodidae 86
Sinocallipus simplicipodus 86
Sinocybe cooki 84
Sinostemmiulus simplicior 85
Siphonophora 84

Source : MNHN, Paris

Siphonophoridae 32, 84, 167, 171
Skleroprotopus confucius 85
Skleroprotopus coreanus 326
Skleroprotopus laticoxalis 85
Skleroprotopus membranipedalis 85
Skleroprotopus serratus 85
Skolopendra (sic!) 26
Spelaeoglomeris alpina 276
Spelaeoglomeris doderoi 276, 504
Spelaeoglomeris jeanneli 276
Speophilosoma 86
Speophilosomatidae 86
Sphaeropauropinae 86
Sphaeropauropus 91
Sphaeropoeidae 84, 166, 171
Sphaeropoeus 166
Sphaeropoeus montanus 166
Sphaerotherium 166
Sphaerotherium cinctellum 619
Sphaerotherium maculatum 166
Sphaerotherium politum 166
Sphaerotherium punctulatum 619
Sphaerotrichopidae 71
Spinotarsus 571
Spinotarsus cuspidosus 571, 573
Spinotarsus tenuis 570, 571, 573, 574
Spirobolellus tatakuwai 85
Spirobolidae 84
Spirobolus bungii 84
Spirobolus cincinnalis 85
Spirobolus exquisitus 84
Spirobolus formosae 85
Spirobolus grahami 85
Spirobolus joannesi 84
Spirobolus umbobrochus 85
Spirobolus walkeri 85
Spirostreptidae 322, 333, 334, 337, 621
Spirostrophus lanyusis 85
Stemmiulidae 524
Stigmatogaster gracilis 600, 601
Stigmatogaster japonica 88
Stosatea italica 245, 246, 247, 248, 250, 258, 277
Streptogonopus phipsoni 75
Strigamia 639
Strigamia acuminata 190, 222, 223, 238, 638, 639, 640, 642, 643, 644, 645
Strigamia crassipes 213, 215, 219, 222, 223, 238, 641, 659
Strigamia engadina 600, 602
Strigamia transsilvanica 238, 601, 603, 638, 639, 640, 641, 642, 644
Strongylomorpha 74
Strongylosoma contortipes 75
Strongylosoma montigena 75
Strongylosoma nadari 87
Strongylosoma pallipes 431, 432, 433, 434
Strongylosomatidae 73, 74
Strongylosomidae 73, 74
Strongylosominae 73
Stygioglomeris crinita 244, 245, 247, 248, 258, 275, 488, 647, 649, 650, 653
Stylodesmoidea 88
Styrioiulus pelidnus 322, 326
Substrongylosoma 170
Substrongylosoma distinctum 76, 170
Substrongylosoma falcatum 76, 170
Substrongylosoma montigena 170
Substrongylosoma schawalleri 170
Sulciferini 74, 86
Suliciferinae 73
Sundanina 74, 75
Sundanina bimontana 75
Sundanina contortipes 75
Sundanina granulifera 75, 76
Sundanina hirta 75
Sundanina jerdani 75
Sundanina laevisulcata 75
Sundanina nitens 75
Sundanina nulla 75
Sundanina pumila 75
Sundanina septentrionalis 75
Sundanina simplex 75
Sundanina trifida 75, 76
Sundanini 74
Symphylella adisi 607, 609, 611, 614
Symphylellopsis 137
Symphyoiulini 315, 324
Symphyoiulus impartitus 326
Symphyopleurium hozawai 84
Syngonopodium 154, 157
Syngonopodium aceris 152, 156
Syngonopodium cornutum 156
Syntelopodeuma gracilipes 86
Syrioiulus cf. *andreevi* 326
Syrioiulus continentalis 326
Szechuanella tenebra 87

T

Tachypodoiulus 322, 324, 325, 373, 374, 382
Tachypodoiulus albipes 190, 193, 199
Tachypodoiulus niger 190, 193, 199, 245, 246, 248, 255, 258, 260, 260, 278, 326, 373, 374, 375, 376, 378, 379, 380, 381, 382, 488, 489, 597, 647, 649, 654
Taiwanella sculptulatus 89
Taiwanella striata 89
Taiwanella yanagiharai 89
Tasmanipatus 142, 148
Tasmanipatus anophthalmus 139, 140, 141, 148
Tasmanipatus barretti 139, 140, 141, 144, 146, 148
Tectoporini 86
Telodrepanum 76
Telodrepanum badaga 75
Telsonemasoma microps 326
Telsonemasomatidae 326
Thalassisobates littoralis 245, 247, 248, 278
Thalthybius boteltoboensis 88
Theatops 294, 295
Thelodesmus 109, 111
Thelodesmus armatus 88, 102

Source : MNHN, Paris

Thereuonema dilatationis 91
Thereuonema hilgendorfi 91
Thereuonema mandschuria 91
Thereuonema tuberculata 91
Thereuonema variata 91
Thereuonema viridescens 91
Thereuopoda clunifera 91
Thereuopoda nivicomes 91
Thracophilus 237
Thracophilus beroni 235, 237, 238
Thracophilus bulgaricus 235, 237, 238
Thracophilus cilicus 237
Thracophilus pachypus 237
Tianella 167, 172, 173
Tianella ausobskyi 167
Tianella bobanga 167
Tianella daamsae 167
Tianella gitanga 167
Tianella jaljalensis 167
Tianella kathmandua 167
Tianella lughla 167
Tianella mananga 167
Tianella mangsingma 167
Tianella martensi 167
Tianella smetanai 167
Tonkinodentus 294, 295
Tonkinosomatini 87
Topalodesmus 169
Topalodesmus communis 169
Topalosoma 170
Topalosoma setiferum 76, 170
Touranella 170
Touranella himalayaensis 170
Trachycormocephalus koreanus 89
Trachydesmus 73
Trachyjulus 168
Trachyjulus mimus 168
Trachyjulus wilsonae 168
Trachysphaera drescoi 271 276
Trachysphaera lobata 245, 247, 248, 249, 276
Trachysphaera pyrenaica 276
Trichoblaniulidae 323,324, 326
Trichoblaniulus hirsutus 278, 326, 596
Trichoblaniulus lanuginosus 278
Trichonemasoma peloponesius 326
Trichonemasomatidae 323, 326
Trichopeltis 168, 171
Trichopeltis watsoni 168, 171
Trichopolydesmidae 71
Trichopolydesmoidea 67, 71
Trichopolydesmus 71
Trigoniophthalmus alternatus 286
Trigoniulus niger 85
Trigoniulus segmentatus 85
Trigoniulus takahasii 85
Trigoniulus tertius 85
Trogloiulus mirus 321
Tygarrup javanicus 89
Typhloblaniulus 592
Typhloblaniulus lorifer consoranensis 381
Typhloiulini 314, 315, 321, 325
Typhloiulus albanicus 321
Typhloiulus ausugi 321
Typhloiulus boldorii 321
Typhloiulus bureschi 321
Typhloiulus illyricus 321
Typhloiulus lobifer 321
Typhloiulus maximus 321
Typhloiulus montellensis 321
Typhloiulus psilonotus 321
Typhloiulus sculterorum 278
Typhloiulus serbani 321
Typhloiulus strictus 321
Typhlopygmaeosoma 169
Typhlopygmaeosoma hazeltonae 169

U

Unciger 314
Unciger foetidus 211, 245, 247, 248, 314, 318, 319, 326, 431, 432, 433, 434, 647, 649, 650, 652, 653
Unixenus 166
Unixenus aff. *broelemanni* 120
Uriunceustreptus afemorispinus 85
Uriunceustreptus retrorsus 85
Uroblaniulus 326
Usbekodesmus 169, 171, 172
Usbekodesmus buddhis 169
Usbekodesmus occultus 169
Usbekodesmus sacer 169
Usbekodesmus theocraticus 169
Usbekodesmus theosophicus 169

V

Vandeleuma vasconicum 277
Vanhoeffeniidae 71
Varyomorpha hsientienensis 87
Varyomorpha pectinata 87
Vascoblaniulus 273
Vascoblaniulus cabidochei 274, 278
Vascosoma coiffaiti 271, 277
Vascosoma coiffaiti falsaforma 277
Vascosoma duprei 271, 277
Venezuelodesmini 67, 71
Venezuelodesmus 67, 68, 69, 70, 71
Venezuelodesmus bordoni 67, 68, 69, 70
Venezuelodesmus decui 67, 68, 69, 70
Venezuelodesmus orghidani 67, 68, 71

X

Xanthodesmini 74
Xanthodesmus physkon 585, 586
Xestoiulus laeticollis 326
Xiphidiogonus 76
Xiphidiogonus dravidus 75
Xiphidiogonus hendersoni 75
Xiphidiogonus spinipleurus 75

Source : MNHN, Paris

Xylophageuma 154
Xylophageuma vomrathi 152, 154, 155, 159
Xylophageuma zschokkei 154, 277
Xystodesmidae 88, 102, 104, 106, 110
Xystodesmoidea 88
Xystodesmus 102, 106
Xystrosoma beatense 277
Xystrosoma cassagnaui 277
Xystrosoma catalonicum 277
Xystrosoma muricum 277
Xystrosoma pyrenaicum 277
Xystrosoma tectosagum 277

Y

Yosidaiulus tuberculatus 326
Yuennanina aceratogaster 86
Yuennanina ceratogaster 86
Yuennanina petalolobodes 86

Z

Zephronia 166
Zephronia alticola 166
Zephronia debilis 166
Zephronia densipora 166
Zephronia disparipora 166
Zephronia hainana 84
Zephronia hirta 166
Zephronia hysophila 166
Zephronia juvenis 166
Zephronia laevissima 166
Zephronia lignivora 166
Zephronia manca 166
Zephronia nigrinota 166
Zephronia profuga 84
Zephronia specularis 166
Zephronia tigrinoides 166
Zephronia tumida 166
Zinophora 337, 621
Zinophora laminata 337
Zosteractinidae 326

BIBL. DU MUSÉUM PARIS
Source : MNHN, Paris

REMERCIEMENTS AUX RAPPORTEURS / *ACKNOWLEDGEMENTS TO REFEREES*

La Rédaction tient à remercier les experts extérieurs au Muséum national d'Histoire naturelle dont les noms suivent, d'avoir bien voulu contribuer, avec les rapporteurs de l'Établissement, à l'évaluation des manuscrits (1988-1996) :
The Editorial Board acknowledges with thanks the following referees who, with Muséum referees, have reviewed papers submitted to the Mémoires du Muséum (1988-1996):

ADKISON D.	Macon	U. S. A.
AFZELIUS Björn	Stockholm	Suède
AKESSON Bertil	Göteborg	Suède
AMIARD Jean-Claude	Nantes	France
ANDRES H.	Hambourg	Allemagne
BABA K.	Kumamoto	Japon
BACHELET Guy	Arcachon	France
BAUD C.A.	Genève	Suisse
BELLAN Gérard	Marseille	France
BEN-ELIAHU Nechama	Jérusalem	Israël
BERGGREN M.	Fiskebackskil	Suède
BERNET-ROLLANDE M. C.	Puteaux	France
BERNOT L.	Anthony	France
BHAUD Michel	Banyuls-sur-Mer	France
BLAKE James A.	Woods-Hole	U. S. A.
BOSS K.	Harvard	U. S. A.
BOURDON R.	Roscoff	France
BOURLIÈRE F.	Paris	France
BOUROULLEC J.	Pau	France
BRESSON F.	Paris	France
BROSSET A.	Paris	France
BURKE Robert D.	Victoria	Canada
BUTLER P. M.	Surrey	Grande Bretagne
BUTMAN Cheryl Ann	Woods-Hole	U. S. A.
CALDE D.	Toronto	Canada
CARRICK Frank	Brisbane	Australie
CASTELLI Alberto	Modena	Italie
CHACE F. A.	Washington	U. S. A.
CHAREST P.	Québec	Canada
CLARK P.	Londres	Grande-Bretagne
COAN E.	Palo Alto	U. S. A.
COMBES C.	Perpignan	France
CORNELIUS P.	Londres	Grande-Bretagne
CORNUDELLA Lluis	Barcelona	Espagne
CUZIN-ROUDY J.	Villefranche-sur-Mer	France
DAVIE P.	Brisbane	Australie
DE BROYER C.	Bruxelles	Belgique
DESBRUYÈRES Daniel	Brest	France
DHAINAUT André	Villeneuve d'Ascq	France
DORRESTEIJN Adriaan	Mayence	Allemagne
DREUX P.	Paris	France
DUCHÊNE Jean-Claude	Banyuls-sur-Mer	France
DUPUIS Y.	Chatenay Malabry	France
EIBYE-JACOBSEN Danny	Copenhague	Danemark
ELDREDGE L. L.	Hawaii	U. S. A.
FAIN A.	Bruxelles	Belgique
FAUCHALD Kristian	Washington	U. S. A.
FISCHER Albrecht	Mayence	Allemagne
FITZHUGH Kirk	Los Angeles	U. S. A.
FLEURY Anne	Orsay	France
FLORET J. J.	Paris	France
FOREY P. L.	Londres	Grande-Bretagne
FOURNIER Judith	Ottawa	Canada
FRANÇOIS Y.	Paris	France
FRANSEN C.	Leiden	Hollande
GAGNÉ R.	Washington	U. S. A.
GAMBI M. Cristina	Napoli	Italie
GÉHU J. M.	Bailleul	France
GENTIL Frank	Roscoff	France
GEORGE David	Londres	Grande-Bretagne
GIANGRANDE Adriana	Lecce	Italie
GIBBS Peter E.	Plymouth	Grande-Bretagne
GILLET Patrick	Angers	France
GLASBY Chris	Canberra	Australie
GLÉMAREC Michel	Brest	France
GOERKE Helmut	Bremerhaven	Allemagne
GOODAY A. J.	Surrey	Grande-Bretagne
GRASSHOFF M.	Frankfurt	Allemagne
GRASSLE Frederick	New Brunswick	Canada
GRASSLE Judith	New Brunswick	Canada
GRUET Yves	Nantes	France
GUGLIELMO L.	Messina	Italie
GUILLAUMET J. L.	Caen	France
HAMLEY Timothy	Brisbane	Australie
HARDEGE Jorg Detelf	Oldenburg	Allemagne
HAYWARD P. J.	Swansea	Grande-Bretagne
HEALY John	Brisbane	Australie
HENSLEY D. A.	Puerto Rico	U. S. A.
HILBIG Brigitte	Massachusetts	U. S. A.
HODGSON Alan	Grahamstown	Afrique du Sud
HOLTE Boerge	Tromsoe	Norvège
HOLTHUIS L. B.	Leiden	Hollande
HOOPER J. N. A.	Brisbane	Australie
HOVE Harry Ten	Amsterdam	Pays-Bas
HUTCHINGS Patricia	Sydney	Australie
JENKINS Farish	Cambridge	USA
JOUIN-TOULMOND Claude	Paris	France
KASINSKY Harold E.	Vancouver	Canada
KENDALL Michael	Plymouth	Grande-Bretagne
KENSLEY B.	Washington	U. S. A.
KIELAN-JAWOROWSKA Z.	Oslo	Norvège
KILBURN R.	Pietermaritzburg	Afrique du Sud
KNIGHT-JONES Phyllis	Swansea	Grande-Bretagne
KNIGHT-JONES Wyn	Swansea	Grande-Bretagne
KOHN A.	Seattle	U. S. A.
KRANTZ G. W.	Corvallis	U. S. A.
KUDENOV Jerry D.	Alaska	U. S. A.
LAGARDÈRE J.-P.	La Rochelle	France
LANA Paulo Da Cunha	Parana	Brésil
LAUBIER Lucien	Paris	France
LAVERDE-CASTILLO J. J. A.	Bogota	Colombie
LE TENDRE L.	Courbevoie	France
LEGAY J. M.	Villeurbanne	France
LEVIN Lisa A.	La Jolla	U. S. A.
MACKIE Andrew	Cardiff	Grande-Bretagne
MACPHERSON E.	Barcelona	Espagne
MANNING R.	Washington	U. S. A.
MARSHALL B.	Wellington	Nouvelle-Zélande
MAUCHLINE J.	Oban	Grande-Bretagne
MAURER Don	Long Beach	U. S. A.
MAXWELL P.	Waimate	Nouvelle-Zélande
MCALPINE J. F.	Ottawa	Canada
MCKENNA M.	New York	U. S. A.
MCLAUGHLIN P.	Washington	U. S. A.
MEISTRICH Marvin L.	Houston	U. S. A.
METTAM Chris	Cardiff	Grande-Bretagne
MUIR Alexander Ian	Londres	Grande-Bretagne
NAGEL P.	Saarbrücken	Allemagne
NEWMAN W. A.	San Diego	U. S. A.
NOËL R.	Pau	France
OLIVA Rafael	Barcelona	Espagne
OLIVE Peter James William	Tyne	Grande-Bretagne
PATERSON Gordon L. J.	Londres	Grande-Bretagne
PATTERSON C.	Londres	Grande-Bretagne
PAXTON Hannelore	North Ryde	Australie
PÉREZ FARFANTE I.	Washington	U. S. A.
PERKINS Thomas H.	Saint Petersburg	U. S. A.
PERTHUISOT J. P.	Nantes	France
PETERSEN Mary E.	Copenhague	Danemark
PETTIBONE Marian H.	Washington	U. S. A.
PEYROT-CLAUSADE M.	Marseille	France
PLEIJEL Fredrik	Stockholm	Suède
POCCIA Dominic L.	Amherst	U.S.A.
POCKLINGTON Patricia	Halifax	Canada
PONTIER J.	Villeurbanne	France
POOR G.	Victoria	Australie
PUIG H.	Paris	France
PURSCHKE Günter	Osnabruck	Allemagne
PUTHZ V.	Schlitz	Allemagne
RAIKOVA Olga	Saint-Pétersbourg	Russie
RAMIL F.	Vigo	Espagne
REISH Donald J.	Long Beach	U. S. A.
RICHER DE FORGES B.	Nouméa	Nouvelle-Calédonie
RIEMAN F.	Bremerhaven	Allemagne
ROUSE Greg	Washington	U. S. A.
SAN MARTIN Guillermo	Madrid	Espagne
SARDA Rafael	Blanes	Espagne
SAVAGE D.E.	Berkeley	U. S. A.
SCHMID M.	Paris	France
SCHROEDER Paul	Pullmann	U. S. A.
SCOTT A. C.	Surrey	Grande-Bretagne
SIBUET Myriam	Brest	France
SIGVALDADOTTIR Elin	Stockholm	Suède
SIMON Joseph L.	Tampa	U. S. A.
SPIRIDONOV V.	Moscou	Russie
STORK N. E.	Londres	Grande-Bretagne
TAKEDA M.	Tokyo	Japon
TAN C. G. S.	Singapore	Singapore
TAYLOR P. D.	Londres	Grande-Bretagne
THURSTON M. H.	Surrey	Grande-Bretagne
TOULMOND André	Paris	France
TRICART J.	Strasbourg	France
TUDGE Christopher	Brisbane	Australie
VACELET J.	Marseille	France
VAN AMERON H. W. J.	Krefeld	Allemagne
VAN SOEST R. W. M.	Amsterdam	Hollande
VOKES E.	New Orleans	U. S. A.
VOVELLE Jean	Paris	France
WÄGELE J. W.	Bielefeld	Allemagne
WARÉN A.	Stockholm	Suède
WARREN Lynda	Cardiff	Grande-Bretagne
WATSON J.	Essendon	Australie
WATSON Nikki	Armidale	Australie
WESTHEIDE Wilfried	Osnabrück	Allemagne
WILLIAMS A.	Washington	U. S. A.
WILSON Robin	Victoria	Australie
WITTMANN K.	Vienne	Autriche
ZEVINA G. B.	Moscou	Russie
ZIBROWIUS Helmut	Marseille	France

Source : MNHN, Paris

Source : MNHN, Paris

ACHEVÉ D'IMPRIMER
EN JUIN 1996
SUR LES PRESSES
DE
L'IMPRIMERIE F. PAILLART
À ABBEVILLE

Date de distribution : 28 juin 1996.
Dépôt légal : Juin 1996.
N° d'impression : 9745.

Source : MNHN, Paris

Source : MNHN, Paris

DERNIERS TITRES PARUS

RECENTLY PUBLISHED MEMOIRS

À partir de 1993 (Tome 155), les *Mémoires du Muséum* sont publiés sans indication de série.
From 1993 (Volume 155), the Mémoires du Muséum *are published without serial titles.*

Tome 168 : Alain Crosnier (ed.), 1996.— Résultats des Campagnes MUSORSTOM. Volume 15. 539 pp. (ISBN : 2-85653-501-1) 538,68 FF.

Tome 167 : Philippe BOUCHET (ed.), 1995.— Résultats des Campagnes MUSORSTOM. Volume 14. 654 pp. (ISBN : 2-85653-217-9) 600 FF.

Tome 166 : Barrie JAMIESON, Juan AUSIO & Jean-Lou JUSTINE, 1995.— Advances in Spermatozoal Phylogeny and Taxonomy. 565 pp. (ISBN : 2-85653-225-X) 440,80 FF.

Tome 165 : Larry G. MARSHALL, Christian DE MUIZON & Denise SIGOGNEAU-RUSSELL, 1995.— *Pucadelphys andinus* (Marsupialia, Mammalia) from the early Paleocene of Bolivia. 168 pp. (ISBN : 2-85653-223-3) 176,30 FF.

Tome 164 : Jeanne DOUBINGER, Pierre VETTER, J. LANGIAUX, J. GALTIER & Jean BROUTIN, 1995.— La flore fossile du bassin houiller de Saint-Étienne. 358 pp. (ISBN : 2-85653-218-7) 479,92 FF.

Tome 163 : Alain CROSNIER (ed.), 1995.— Résultats des Campagnes MUSORSTOM. Volume 13. 518 pp. (ISBN : 2-85653-224-1) 550 FF.

Tome 162 : Jean-Claude DAUVIN, Lucien LAUBIER & Donald J. REISH (eds), 1994.— Actes de la 4ème Conférence internationale sur les Polychètes. 642 pp. (ISBN : 2-85653-214-4) 390 FF.

Tome 161 : Alain CROSNIER (ed.), 1994.— Résultats des Campagnes MUSORSTOM. Volume 12. 569 pp. (ISBN : 2-85653-212-8) 600 FF.

Tome 160 : Nicole BOURY-ESNAULT, Maurizio PANSINI, & Maria Jesus URIZ, 1994.— Spongiaires bathyaux de la mer d'Alboran et du Golfe ibéro-marocain. 174 pp. (ISBN : 2-85653-213-6) 300 FF.

Informations sur les Publications Scientifiques du Muséum national d'Histoire naturelle :
Informations about the Scientific Publications of the Muséum national d'Histoire naturelle:
Internet http://www.mnhn.fr/

Prix hors taxe, frais de port en sus. Vente en France : TVA 2,10%.
Prices in French Francs, postage not included.

Source : MNHN, Paris

This volume represents a fundamental contribution to our knowledge of myriapod and onychophoran biology. It is divided into eight sections, dealing with the following topics: Historical Myriapodology; Advances in Systematics and Biodiversity; Systematics, Evolution and Phylogenetic Relationships; Community Studies and Biogeography; Reproductive Developmental Trends; Physiology, Ecophysiology and Cell Biology; Population Biology, Soil Ecology and Behaviour; Communities in Ecosystems.

The text includes 79 contributions from 107 authors and should prove essential reading for all students and researchers of the biology, ecology and systematics of Diplopoda, Chilopoda, Symphyla, Pauropoda and Onychophora.

Jean-Jacques GEOFFROY is a researcher of the Centre national de la Recherche scientifique. He works at the Muséum national d'Histoire naturelle, General Ecology (Brunoy, France), on population ecology in forest soils, biogeography and biodiversity, mainly on the arthropod groups Diplopoda and Chilopoda.

Jean-Paul MAURIÈS is Maître de Conférences at the Muséum national d'Histoire naturelle, Zoology/Arthropods (Paris, France). A Diplopoda taxonomist, he has mainly published papers on holarctic and pantropical forms, with special reference to problems of speciation and biogeography of millipedes, connected with their habitats in islands, caves and mountains.

Monique NGUYEN DUY - JACQUEMIN is a researcher of the Centre national de la Recherche scientifique. She works at the Muséum national d'Histoire naturelle, Zoology/Arthropods (Paris, France), on development, sensory organ ultrastructure and taxonomy of Diplopoda. She is a specialist of the millipede group Penicillata.

ÉDITIONS
DU MUSÉUM
57, RUE CUVIER
75005 PARIS

ISBN 2-85653-502-X
ISSN 1243-4442

550 FF TTC (France)
538,69 FF HT (Étranger)

Source : MNHN, Paris